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CONTENTS.

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CONTRIBUTIONS TO THE COMPARATIVE OSTEOLOGY OF ARCTIC AND SUB-ARCTIC WATER-BIRDS. PART I.

By R. W. SHUFELDT, M.D., C.M.Z.S.

(PLATES I., II., III., IV., V.)

SEVERAL years before his death, Professor Spencer F. Baird placed in my charge for description a very extensive collection of skeletons of many of the Arctic water-fowl, representing the majority of the genera of Divers, Gulls, Auks, and Auklets, inhabiting the polar and sub-polar seas of both Continents. Most of this fine array of material had been collected in Alaska and elsewhere, by such well-known explorers as Henry W. Elliot, Dall, T. H. Bean, and others, and subsequently stored away in the vast collections of the Smithsonian Institution at Washington, where I first came across it. Still later, Mr W. A. Forbes, then Prosector of the Zoological Society of London, and just before his ill-fated African trip, sent me some fine skeletons of *Alca torda*, and many valuable notes in his letters written to me prior to the time I mention. Finally, my own private collection yielded the skeletons of several forms of birds of the same order I allude to; and lastly, I have enjoyed the rare opportunity, through the kindness of Mr F. A. Lucas of the United States National Museum, to examine two fine skeletons of the extinct Great Auk (*Plautus impennis*), recently collected by him on the islands at the mouth of the St Lawrence River, and submitted to me for that purpose.

Further, I must here thank my friend Dr T. H. Bean for his present of four fine heads, in alcohol, of an albatross from the same region (*Diomedia brachyura*). Shortly after all this

material came into my possession, I was called away to be absent several years in New Mexico, and while this gave me the opportunity to carefully overhaul my treasures, and make a very complete set of drawings of all the subjects in the collection demanding it; it, on the other hand, when I came to write out my observations, debarred me from going over much work already done and published by others in the same fields. For this last unavoidable drawback I must be pardoned, the more especially if, in any particular instance, I seem to ignore the labour of other biologists.

The drawings illustrating my now well-digested work upon this material were all executed by myself, though in a number of the figures in the text, the stipple-shading was filled in to my outlines by my wife, under my supervision, for which patient labour my most grateful acknowledgments are due. The platse were all done by myself direct from the specimens they represent.

As it has been found necessary to refer to some recognised classification of birds as a basis, I have chosen the system adopted by the American Ornithologists' Union, as set forth in *The American Ornithologists' Union Code and Check List of North American Birds*, and will, throughout, adhere to the nomenclature there given.

As this work will extend through several parts, I have found that it has been necessary, in order to introduce all my figures, both in text and plates, to occasionally bring in a figure before it has been described in the text, or perhaps allude to one in a "Part" before it appears; but all this will be clear to the reader when the work is entirely completed and fully out. In the case of the plates, it could not well be avoided, as they had to be arranged according to the space.

Through the labours of Sir Richard Owen, Wyman, E. Blyth, and others, the osteology of the extinct Great Auk is now well known to anatomists; and I understand from Mr Lucas that he intends to fully describe the magnificent additions he has been enabled to make in that direction, in the way of a number of nearly complete skeletons, and many parts of the same; so that I will hardly feel at liberty to very fully touch upon the material he has so kindly placed at my disposal. I may say here, however, that I have never been able to understand why Owen compared the skeleton of the Great Auk with the bird he did, in his memoir on the subject, in the fourth part of the fifth volume of the *Transactions of the Zoological Society of London*. The most superficial examination is sufficient to convince any one that the nearest kin of the Great Auk is seen in the existing *Alca torda*, and *Cepphus grylle*, the species Owen used in his com-

parison, belongs to another subfamily, it being a Guillemot, and not an Auk at all. Among my plates I have reproduced a few of Owen's figures for comparison in the present connection, choosing them from the monograph to which I have just alluded.

Professer E. D. Cope of Philadelphia has, in his renowned paleontological collections, many fossil and sub-fossil skeletons of water-birds from this country; and, several years ago, he kindly promised to allow me to compare them in the present connection; but circumstances, to which I have already referred, prevented me from availing myself of so rare an opportunity, and to throw, perhaps, some light on the subject of the affinities of the existing and extinct types; nevertheless, I feel my thanks are due to him for so distinguished an offer. It will be my intention in this work to first give a full description of the skeleton of an adult specimen of a good representative of the subfamily *Alcinæ*, which contains the Murres, Guillemots, and all the Auks proper.

We will then have a basis for comparison both as to general characters and minor details. The data thus obtained I will endeavour to present in such a shape as to render it easily available for just such comparison with the forms that will be afterwards taken up. For the next thing to be done, after this, will be to take up the representative of a near-related genus of Auks, and compare its skeleton with the one that I have chosen to stand as our model, and in whose skeleton we are to find the general features of this part of the anatomy of an Auk. The form I intend to utilise to this end is the skeleton of *Alca torda*, the well known Razor-billed Auk. After the *Alcinæ* have thus been dealt with, and all the material at my command fully compared and tabulated, I will pass to the consideration of the next subfamily in order, the *Phalerinæ*, containing the Auklets and other forms, which I will treat in a like manner, comparing them with the first group examined.

For the sake of convenience and of reference, it may be just as well here to present the classification of the *Alcidæ* as adopted by the American Ornithologists' Union at present.

Very properly the *Check-List* starts with those birds in the avifauna of North America which are supposed to hold the lowest position in the scale of organisation, so that we find the first in order to be the *Pygopodes* or Diving Birds. The first division under this is the suborder *Podicipedes*, or the Grebes; and next the family *Podicipidæ*. Overlooking the subgenera, we find this first family of the *Pygopodes* divided into three genera, which I present with the species under each:—

Genus *Æchmophorus*.

1. *Æ. occidentalis*. Western Grebe

Genus *Colymbus*.

2. *C. holbœllii*. Holbœll's Grebe.
3. *C. auritus*. Horned Grebe.
4. *C. nigricollis californicus*. American Eared Grebe.
5. *C. dominicus*. St Domingo Grebe.

Genus *Podilymbus.*

6. *P. podiceps.* Pied-billed Grebe.

Then follows :—

Suborder CEPPHI. Loons and Auks.

Family URINATORIDÆ. Loons.

Genus *Urinator.*

7. *U. imber.* Loon.
8. *U. adamsii.* Yellow-billed Loon.
9. *U. arcticus.* Black-throated Loon.
10. *U. pacificus.* Pacific Loon.
11. *U. lumme.* Red-throated Loon.

Then follows our Alcidæ:—

Family ALCIDÆ. Auks, &c.

Subfamily FRATERCULINÆ. Puffins.

Genus *Lunda.*

12 *L. cirrahata.* Tufted Puffin.

Genus *Fratercula.*

13. *F. arctica.* Puffin.
13*a*. *F. arctica glacialis.* Large-billed Puffin.
14. *F. corniculata.* Horned Puffin.

Subfamily PHALERINÆ. Auklets, Murrelets, Guillemots.

Genus *Cerorhinca.*

15. *C. monocerata.* Rhinoceros Auklet.

Genus *Ptychoramphus.*

16. *P. aleuticus.* Cassin's Auklet.

Genus *Cyclorrhynchus.*

17. *C. psittaculus.* Paroquet Auklet.

Genus *Simorhynchus.*

18. *S. cristatellus.* Crested Auklet.
19. *S. pygmæus.* Whiskered Auklet.
20. *S. pussilus.* Least Auklet.

Genus *Synthliboramphus.*

21. *S. antiquus.* Ancient Murrelet.
22. *S. wumizusume.* Temminck's Murrelet.

Genus *Brachyramphus.*

23. *B. marmoratus.* Marbled Murrelet.
24. *B. kittlitzii.* Kittlitz's Murrelet.
25. *B. hypoleucus.* Xantus's Murrelet.
26. *B. craveri.* Craveri's Murrelet.

Genus *Cepphus.*

27. *C. grylle.* Black Guillemot.
28. *C. mandtii.* Mandt's Guillemot.
29. *C. columba.* Pidgeon Guillemot.

Subfamily ALCINÆ. Auks and Murres

Genus *Uria.*

30. *U. troile.* Murre.
30*a*. *U. troile californica.* Californian Murre.
31. *U. lomvia.* Brünnich's Murre.
31*a*. *U. lomvia arra.* Pallas's Murre.

Genus *Alca.*

32. *A. torda.* Razor-billed Auk.

Genus *Plautus.*

33. *P. impennis.* Great Auk.

Subfamily ALLINÆ.

Genus *Alle.*

34. *A. alle.* Dovekie.

Next follows the order Longipennes, containing the Jaegers, Skuas, and the Gulls and Terns. Then come other orders of the water-fowl, too full to be quoted here, and the reader, if he wish to pass them in review, as the Union arranges them in the first edition of the *Check-List*, is referred to that volume for the purpose.

As I have already said in a preceding paragraph, after dealing with subfamily Phalerinæ, we will take up, as the material and types seem best to suggest, other forms of these birds, and submit them to similar comparisons with the data already obtained. Let us now return to the consideration of the skeleton of *Alca torda*, with a word first about the habitat and external characters of this Auk.

Razor-bills are found in immense numbers in certain localities in the Polar Seas, and on the coasts of the North Atlantic Ocean. Stragglers from these parts are occasionally taken in the North Pacific and elsewhere. Upon the authority of Coues, the external characters of the genus *Alca torda* are as follows :—" Size, form, and general aspect of the last genus [*Uria*]. Bill about as long as head, densely feathered for half its length, the feathers extending on upper mandible beyond middle of commissure, those on lower somewhat

farther. Bill greatly compressed, cultrate, sulcate, hooked; culmen ridged, regularly convex; commissure straight to the hook; gonys about straight. Nostrils linear, marginal, densely feathered. Tarsi scutellate in front. Tail short, pointed, of stiffish, acute feathers. Wings normal, effective for flight. Bicolor. Egg single, colored. One species." (Key, 2nd ed. p. 818.)

Of the Skeleton of Alca torda.

Under each genus or group discussed in this memoir, it is my intention to present in a tabulated form the material that I had at hand for investigation at the time it was written, its condition, source, and other matters. As an example of this I here subjoin such a table containing the material examined in the present connection.

Tabulated List of Material.

Specimen and Sex.	Condition, &c.	Complete or Incomplete.	Source.	In whose possession at present.
Alca torda.	Dried and perfectly cleaned skeleton. ♂	Hyoid arches, sclerotals, and number of small bones missing.	From the late W. A. Forbes, Prosec. Zool. Soc. of London.	Dr R. W. Shufeldt.
Alca torda.	Skull, cleaned and bleached.	Bones of the sense capsules, &c., missing.		

It will be seen from this table that the hyoid arches are really the greatest defect in this specimen, and the general character of these I can give elsewhere further on, as found in the Guillemots and others.

Of the Skull.—In Plate I. figs. 1 to 4 inclusive, I have drawn different views of the skull and mandible of the Razor-billed Auk, choosing for my subject the female specimen in the above table. This was done because it seemed to be a larger and better skull, and more perfect in some of its details.

Huxley gives us a very good figure of the inferior view of the skull of this bird in his "Classification of Birds" (*Proc. Zool. Soc.*, 1867), comparing it with the basal view of the skull of *Larus rissa;* both of these forms falling in the order *Schizognathæ*, being grouped with other water-birds, as the *Colymibidæ* and

Procellariidæ in the *Cecomorphæ* of the arrangement proposed by this writer.

Upon lateral view of the skull of this Auk (Pl. I. fig. 1), we are at once struck with the large opening of the osseous nostril on the side of the superior mandible. This is rounded in front, and carried up into the slit of the nasal behind. There being not a vestige of such a thing as a nasal septum in *Alca torda*, one has a perfectly uninterrupted view through these nasial apertures from side to side. The anterior extremity of this mandible is hooked, with the hook directed downwards and forwards. Its lower border, from the maxillary to the tip of this hook, is sharp, being gently convex downwards until well past the opening of the nostril above it, when the reverse and more abrupt curve is seen to the tip of the beak. At a point anterior to the middle of the nasial opening, the mandible above gently rises to form a regular convexity with rounded culmen, which slopes away on this aspect to the tip of the mandibular hook. Behind this the surface of the mandible is on a lower level, lower even than the frontal region, and but slightly curved from side to side. The lateral aspect of this vaulted anterior part of the mandible is flat, and marked by a marginal row of foramina, with a few scattered ones above them.

As with most Schizorhinal birds, this condition of the nasal in *Alca* can be seen on this view. The maxillary fork of the bone, however, is the one to be spoken of here. This is of about an equal width throughout its length. Its superior end is flattened, overlaps the lacrymal and faces directly to the front; the remainder of this part often has a lateral aspect, and merges below into the dentary process of the premaxillary, making a posterior angle with the maxillary of about 45 degrees.

The anterior part of the suture between the jugal and the maxillary is persistent, the former overlapping the thin horizontal plate of the latter. For the remainder of the bar, it is strong, and articulates with the quadrate in the usual way; the quadrato-jugal end being slightly bent upwards, and its peg-like process at right angles to the inner aspect of the distal end of the bone.

The *lacrymal* is overlapped by the nasal in front as described above; its inner margin bounds the large superorbital foramen,

which bears an outer postero-superior process to assist in forming the periphery of the orbit in continuation with the frontal. Then it sends down a styliform process, directed slightly backwards, towards the jugal bar. The inner aspect of the middle third of this descending process of the lacrymal, anchyloses with the outer margin of the pars plana, thus creating a foramen above and an arch below, which latter is formed by the lower concave margin of this ethmoidal wing.

Alca has at the extreme end of this descending process of its lacrymal a diminutive articular facette intended for articulation with a small hook-like bone, which I take to be the "os uncinatum." This fragile and free bone is shaped like an L, being very thin, with its surface directed forwards and backwards. One limb, the horizontal one, after articulating with the facette on the end of the lacrymal, has its upper border for its entire length resting against the lower border, as far as the limb extends, of the ethmoidal wing. The vertical limb of the os uncinatum reaches down to rest by its lower apex on the jugal bar. It will be seen that the arrangement of this little bone is quite different in the Albatross. I take this to be the "os uncinatum," from Parker's description of it, who also calls it the *antorbital*, and says:—"Unlike its congeners, the Cariana has its nasal septum but little ossified, and it possesses an 'os uncinatum' propping up the pars plana, as in the Gull, Albatross, and many other birds" (*Ency. Brit.*, 9th ed., art. "Birds"). It has never been my fortune to have seen Professor Reinhardt's paper upon this bone, published in 1871.

The outer periphery of a little more than the upper half of the orbit in this, as in many other Auks, is very distinctly defined, it being a prominent rim running all the way around, from the lower tip of the sphenotic process to the corresponding tip of the lacrymal. It is principally the superorbital glandular depressions that give these orbital peripheries their undue prominence, added to the peculiar ring-like sphenotic process, which is extended so far laterally as to support the continuation of this rim behind, allowing it to form one unbroken curve between the two points mentioned. Almost equally prominent is the squamosal process in this Auk, so that the valley between it and the aliform sphenotic is deep and circularly concave; the

wing behind the auditory opening, whose outer margin is continuous with the former process, is also well developed. We may note likewise on this lateral view of the skull of *Alca torda*, the hemiglobular parietal region of its vault, the supraoccipital prominence, and the deep crotaphyte fossa between these two.

The *interorbital septum*, as well as the inner posterior wall of the brain case, has several large deficiences in them. In the case of the septum, a large quadrilateral one occupies the centre of the plate, while the greater part of the track of the olfactory nerve is also cut through. The foramen for the optic nerve may be distinct, or it may merge into the smaller nerve foramina lying to its outer side. The foramen ovale is large, elliptical, and a plane passed through its periphery would look downwards, forwards, and outwards.

Between the orbital cavity and the rhinal chamber the ethmoidal wing here forms quite a thorough partition. One foramen above it has already been described; it has another, through which the olfactory passes, situated at its upper and inner angle.

As in most other *Alcidæ*, the *quadrate* of the Razor-bill is a large and well-developed bone. The extremity of its lamellaform and broad orbital process is truncate and rounded off, while the body of the process itself is concavo-concave, being bent anteriorly. The upper end of the quadrate supports two articular heads, with a rounded notch between them. Its mandibular foot has two distinct facets for the lower jaw. The inner of these is small and is at the same time the lower of the two. The outer one is placed obliquely on the bone, with its broadest and convex portion forwards and outwards, the quadrato-jugal articulating just above it laterally. Between these two facets a shallow notch occurs. Smaller than either is the pedunculated articular process of the quadrate for the pterygoidal cup, situated on the end of that bone.

On the *basal view* (Pl. I. fig. 3) of the skull of *Alca torda* we are to note principally the long, median open space forward of the vomer, and between the anterior ends of the palatines and the dentary processes of the premaxillary. This opening is rounded in front and broader behind. The outer edges of the premaxillary are slightly raised and rather sharp, overlapping

the horizontal plates of the maxillary on either side behind. This part of the maxillary is not perforated by a foramen, as it is in many birds, but is insinuated between the nasal and dentary process of the premaxillary, as in all true *Schizognathous* forms. At this juncture it throws off the maxillo-palatine plate, which is here a subcircular disc, concave on its under side, the reverse above, obliquely inclined, so its external or lower aspect faces downwards and outwards. Anteriorly, a maxillo-palatine unites with the inner side of the nasal and the upper surface of the palatine of the same side. It does not touch the vomer or the fellow of the opposite side, however, but is separated from either by quite an interval. These plates are smooth, and composed of compact tissue, with not the slightest tendency to sponginess.

The "maxillary process" of a *palatine* is long and slender, its anterior end merging with the dentary process of the premaxillary in the same horizontal plane, while upon its superior aspect, just before this union takes place, the maxillary and maxillo-palatine is seen to unite with it.

The body of the bone is not very wide, and the internal and external laminæ but fairly developed. On referring to the figure, we also observe that the postero-external angle is rounded, and a small foramina may, in some specimens, perforate the external lamina just within it.

In the median line the entire inner aspects of the "pterygoid processes" of the palatines, as well as the entire surfaces of the inner lamination of each beautifully scroll-like "ascending process," are closely applied to each other. This forms in the middle line a sharp carination which is carried forward, on its under side, to the very tip of the decurved *vomer*.

This latter bone is pointed in front, a point which is formed by the meeting of the margins of the outer sides of the longitudinal groove which traverses it above, and the carination just described. This superior groove is continuous behind with a similar one formed by the united palatines; the whole forming an articulation for the under side of the rostrum. The sides of the vomer are continuous with the inner walls of the anterior projections of the "ascending processes" of the palatines, the sutural lines being completely obliterated.

The rostrum is only moderately strong, being carried forwards in front in the form of a delicate spicula of bone, which lies in the upper groove of the vomer, from its posterior half. Behind this, its inferior surface is subcylindrical.

Anteriorly, the heads of the *pterygoids* are in contact and extensively articulate with the palatines. Above they contribute a part to the median longitudinal groove formed by the palatine and vomer for the rostrum.

The shafts of the pterygoids are so bent as to be convex along their inner aspects, where they are longitudinally excavated, and concave from one extremity to the other along their anterior faces. Their proximal ends are elliptically dilated to accommodate a cup for the facet on each quadrate.

A delicate lip of bone overhangs the common orifice of the Eustachian tubes on the basi-sphenoid.

This latter region is wide from one auricular depression to the other, but narrow antero-posteriorly. The usual foramina for the carotids and nerves pierce it at the sites commonly seen in birds at large. The occipital condyle is of good size, very faintly notched above; makes but slight encroachment on the periphery of the foramen magnum; and may be otherwise characterised as a sessile hemi-ellipsoid, placed transversely in the median line with its convex surface outwards.

In the skull of my female specimen of this Auk, I find a sub-elliptical foramen magnum measuring 9 mm. across and 5 mm. from above downwards in the median line, while the corresponding measurements in the male specimen are 8 mm. and 6 mm. This gives a much more circular aperture, quite apparent upon the most casual inspection.

I believe the individual differences among birds' skulls are much greater sometimes than we imagine. Any one who has had the opportunity to examine a series of skulls of the human subject, chosen from the same race of people, and even of the same sex, can hardly help being struck by the very decided individual differences existing among them,—differences sometimes almost amounting to more than specific distinction. It is more than likely that this obtains throughout the vertebrate series,—indeed, I have often noticed it among mammals and birds, and in the Alligator among the reptiles.

The plane of the foramen magnum in the Razor-bill makes an angle with the basis cranii of about 45 degrees.

Viewing the skull from above (fig. 4), we are to note the great lateral compression of the superior mandible anteriorly as compared with its depth as we saw it upon lateral aspect. More posteriorly we see how well this Auk exemplifies the typical schizorhinal bird.

The splitting of the nasals is distinctly seen, and their boundaries can almost be defined in the adult as well as the nasal processes of the premaxillary. This region rests upon the broad abutment of the ethmoid, which spreads out beneath it on the under side. We find also that this latter bone is cut across transversely over the line of the cranio-facial hinge. This section gives rise to a free triangular piece of bone—marked by a longitudinal crest which is the continuation of the anterior median crest of the ethmoid—lying just beneath the nasal processes of the premaxillary.

The *supraorbital glandular depressions* are very deep in this Auk; they are separated in the median line by an elevated thin lamelliform crest of bone, while posteriorly they are riddled with foramina. A single and large one of these apertures occurs at the antero-external angle of each glandular depression that is constant. It has a rounded anterior border, and a jagged posterior one.

In the drawing of *Plautus impennis* of Professor Garrod, I see that these last-mentioned foramina occupy rather more than a third of each depression in question, the form of each aperture being similar in outline (*Col. Sci. Mem.*, p. 125, fig. 1). On the other hand, in the superior aspect of the skull of this extinct Auk, as given by Owen, we see that these openings are quite small, and no larger than I have drawn them in *Alca torda* (*Trans. Zool. Soc.*, vol. v. pl. li. fig. 2). So they must have greatly varied in size in the Great Auk, presuming the drawings of these two anatomists to be correct in this particular, and taken from different specimens.

These large glandular depressions in front in connection with the extensive crotaphyte fossæ behind, leaves but a limited area of the smooth vault of the skull. This has the form of an ace of spades, with its apex in the median line continued forwards by the crest between the glandular fossæ, while its handle is the

isthmus of isolation between the crotaphyte depressions behind. It is marked by a shallow longitudinal gutter. The raised rims of the orbits have already been sufficiently described above. At the sides, the brain case is smooth and semi-globular.

The crotaphyte fossæ are bounded behind by a raised and sharpened crest, running from a central point on the upper side of the wing over the auricular opening to the outer posterior angle, on either side, of the handle of the above-described ace of spades.

This crest forms one of the most prominent features of the *posterior aspect of the skull*, where it bounds a semicircular area, in which is found the foramen magnum and the major part of the supraoccipital prominence.

This latter elevation, the bony vault covering the cerebellum, is in this Auk very large, its upper portion lying beyond the above-mentioned crest in the rounded inner terminations of the crotaphyte fossæ.

It is pierced, on either side, by a large subelliptical foramen, the minor axes of which are in the horizontal plane. My female specimen shows this, while in the male only one small foramen occurs on the left side, close up near the crotaphyte crest.

Some authors are inclined to attach considerable importance to these supraoccipital foramina, as to their being present in some birds and absent in others. After a careful examination of a long series of skulls in which they are frequently to be found, I have come to the conclusion that they are by no means a constant character—and a thoroughly unreliable one—for any classificatory purposes whatever, even among species.

It is to be noted on the lateral view of the *mandible* (figs. 1 and 2), that the posterior angular process is sharp and recurved, though hardly carried above the articular facets. Beyond and anterior to this, on the side of the bone, there is an elongated process, the upper side of which supports a part of the articular surface for the outer facets of the quadrate. Still more anteriorly, the mandible becomes flatter and deep; it is here pierced by an elliptical foramen, of some size, placed longitudinally. This is not the usual normal vacuity that occurs in the splenial slit in many birds. Such sutural traces of this latter feature are also present in *Alca*, being distinctly seen, but the bones have crowded together, and no opening exists in the locality. Beyond,

the mandible becomes narrower, and longitudinally excavated, which excavation gives rise to a prominent rounded superior border, but terminates in a point some considerable distance before reaching the apex of the symphysis.

The end of the mandible is obliquely truncate, from the tip backwards—the lower angle being rounded off, and the bone deeper from above downwards just opposite that point.

Fig. 2 will, perhaps, give a better idea of the appearance of this bone, as seen from above, than any verbal description can do. It will be seen that the inner processes of the articular ends hook forwards, and that their pneumatic foramina are very small. The coracoid processes are but feebly developed, and the ramal borders upon which they are placed, broadly rounded off. This is not so marked beyond, while opposite the comparatively short and depressed symphysis, they are raised and sharp. The posterior aspect of the proximal end of a ramus presents a triangular depression with its apex below; this depression is formed by the intersection of two convex raised and prominent lines, one, the longer, coming from the tip of the inner articular process,—the other, descending from the apex of the posterior articular process. Inner and outer surfaces are thus created on the lower side of each articular end—they being divided by a longitudinal line passing from the apex of the above-mentioned triangles to merge into the contiguous lower and rounded ramal borders.

Each lower ramal border when within a short distance of the symphysis thickens on its inner aspect. The convexity thus formed, being opposite the one similarly situated on the other ramus, gives rise to a constriction in the angular aperture of the mandible at this point, which is quite characteristic of many of these birds (fig. 2).

For the most part, the anterior halves of the inner ramal walls are smooth, each being in this region convex both from above, downwards, as well as longitudinally. Their proximal ends, more especially in the region of the elliptical vacuity, above described, are excavated on these aspects.

As I have attempted to describe it, this, then, is the mandible of a typical Auk; it will, however, be often deviated from as we come to examine the same bone in other members of the sub-

family *Alcinæ*. As a rule, though, the fundamental features will be about the same, and indeed, it will also be observed that in birds more remotely connected, many of these characters will be found to persist in them.

I am sorry to say that the skeleton of the hyoid arches in both of these specimens of *Alca torda* have been lost. Though this prevents me from describing it for this particular Auk, I can still present its general features as found in many other related forms, as the Guillemots, Puffins, and others; so the characters it no doubt has in the Razor-bill can be easily suspected.

Of the Vertebral Column.—Professor Owen, in describing the vertebral column of *Plautus impennis* in the *Transactions of the Zoological Society*, says:—

"In the present specimen there are twenty-two moveable vertebræ between the skull and sacrum, the last nine supporting moveable ribs, of which the first two pairs have free extremities; the succeeding pairs of free pleurapophyses articulate with hæmapophyses and these with the sternum."

"The sacrum appears to include fourteen vertebræ, of which the first supports a tenth moveable pair of ribs, the last of the ordinary thoracic costal series; its hæmapophysis does not reach the sternum. The caudal vertebræ are fourteen in number, of which the last three are blended together, and the first, by its pelvic relations, might claim to belong to the sacral series."

Alca torda agrees with this description in every particular, with the exception of the number of caudal vertebræ. This Auk, or at least my specimen of it, seems to possess but eight free caudal vertebræ and the pygostyle. How many this latter segment contains, I am unable to say from the consolidated bone in the adult. Possibly it may contain six more vertebræ, but it does not appear to have more than four, or at the most five.

The *atlas* in the Razor-bill has its cup perforated at its base by the "odontoid process" of the second vertebra. Its neural canal is large and broadly elliptical, and a stumpy diapophysis is directed backwards and slightly outwards from its arch on either side. An aborted, bifid hypapophysis overlaps the centrum of the axis, when these two vertebræ are naturally articulated.

The second, third, and fourth vertebræ all have lofty neural spines, far-spreading and up-tilted transverse processes, and all possess well-developed hypapophyses situated far back upon their respective centres. The first of these has its centrum

compressed from side to side, and offers the usual articulatory facets for articulation with the atlas. The third and fourth vertebræ are very broad transversely, as are these segments throughout the column. They have pleurapophyses as long as their bodies, pointed directly backwards, and both enclose, or assist to enclose, cylindrical arterial canals for the vertebral arteries. The neural canal is circular throughout the cervical series of vertebræ, and very large.

In the fourth vertebra we find an exceedingly delicate spicula of bone on either side, connecting the pre- and post-zygapophyses. We find in the fifth vertebra an elongated and shallower hypapophysis, but this process does not occur again until we find a broad, deep median one in the tenth vertebra; the sixth, seventh, eighth, and ninth vertebræ being grooved for the carotid arteries, the sides of these grooves never meeting in the median line so as to form a "carotid canal." Neural spines are absent from these neck segments through the fifteenth, and the pre- and post-zygapophyses are broad and spreading in the same. The pleurapophyses become shorter as we proceed backwards to form a small pair of free ribs for the first time in the fourteenth vertebra. The eleventh and twelfth segments have single hypapophyses, as we found it in the tenth, only rather smaller. Initial steps are taken on the part of the thirteenth, fourteenth, and fifteenth vertebræ towards forming a spreading, bicornuate hypapophysis which appears in the sixteenth. In the next behind, or the seventeenth, its pedicle is longer, to be still longer in the eighteenth, where it nearly loses its cornua entirely, they being reduced to two spiculæ projecting forwards. This process then as we proceed backwards becomes progressively shorter in each vertebra, to disappear in the last free one, where it is quite short and inconspicuous. The articulations of the centra of the last six dorsal vertebræ is of the opisthocœlous type. Metapophyses and other ossified spiculæ lace these free rib-bearing vertebræ of the dorsal region above. Quadrilateral neural spines of an equal height are also seen here, the first one being on the fourteenth vertebra is rather small, but they soon become nearly equal in size, and slightly interlock at their upper antero-posterior angles.

The ribs on the fifteenth vertebra, though they support free unciform appendages, their extremities are not connected with the sternum by costal ribs.

These *unciform appendages* in this Auk are all freely articulated with the ribs upon which they occur. They are long and narrow, overlapping in mid series at least two of the ribs behind the one to which the appendage is attached. The last pair of ribs, coming from beneath the ilia, never have these processes, but the pair of ribs anterior to these may or may not show abortive evidences of their presence. Ribs in Auks, both costal and vertebral, have a peculiar style of their own. From before backwards both kinds become gradually longer and more sweeping, their hinder ends being found some distance behind the pelvis. This arrangement can best be appreciated by the study of the trunk skeleton of one of these birds, such as Owen's figure of the Great Auk's skeleton in his memoir upon that fowl, or fig. 32 of Plate V. accompanying this memoir. The last costal rib that reaches the sternum in *Alca torda* has a length of nearly 7 centimetres. The pelvic bones, or more properly the ilia, overlap three pairs of these vertebral ribs, the anterior pair being attached to the last free vertebra, the next two with the sacrum, the last pair of which may anchylose with it.

I fail to find pneumatic foramina in any of these vertebræ, and if they do exist they must be very small.

Marsh found in the extinct *Hesperornis regalis* twenty-three vertebræ between the skull and sacrum; the eighteenth one being the first to meet the sternum through the intervention of a costal rib, and the three preceding the eighteenth had free ribs. The co-ossified sacral series contained fourteen, and there were twelve more in the tail. Thus there were forty-nine vertebræ in the column of this extinct diver.

It will be well to remind the reader here, too, that these bones in *Hesperornis* were also non-pneumatic.

With the exception of the number in the sacrum, it will be seen that the other regions of the column, as well as the total number of vertebræ, differed in the Auks and *Hesperornis*.

Plautus impennis, *Alca torda*, and *Hesperornis regalis* all have, however, fourteen vertebræ, co-ossified with the pelvic bones.

When I come to examine other Auks further on, and look into the number of vertebræ contained in the vertebral columns of existing *Pygopodes,* this matter will be brought up again.

Of the Pelvis.—One of the first things that strikes the eye upon superior view of the pelvis of this bird is its great length over its width. In contradistinction with some of the divers, this is not due here to the long ilia, but partly to that and partly to the extension backwards of the long post-pubis on either side.

The preacetabular part of an ilium is a delicate leaflet of bone, with a rounded and serrated anterior border, while its lateral margins are thin and brittle in the prepared skeleton. This portion of the bone is widest in front, but gradually contracts as it nears the acetabular region. Internally, its free margins do not touch the neural crest of the united pelvic vertebræ, and in consequence we find open "ilio-neural grooves." Posterior to an acetabulum we find in the horizontal plane a small area of this bone, which is obliquely marked by a muscular line. It is on the lateral aspect of the pelvis, however, that the major part of the ilium is seen to the rear of the cotyloid cavity. The form and limits of the neural spine of the first vertebra that anchyloses with the sacrum can easily be made out. In the three following they indistinguishably unite to make a solid crest that continues the disjointed one of the dorsal region. After that, the sacrum lacks a neural crest, and at first is convex and broad, to become concave and progressively narrower as it nears the caudal extremity.

The transverse processes of these ultimate seven vertebræ are simply thrown out to abut against the inner margins of the ilia, the union between these extremities and the free iliac edges being very feeble. These diapophyses are perfectly distinct, and consequently leave a double row of "sacral foramina" down the dorsal aspect of the pelvis.

Upon lateral views (figures of the pelvis will be given in a subsequent Part) we are still reminded of the general appearance of weakness which is characteristic of the pelvis of many of the Auks, pointing to the fact that the bird is not gifted with any great powers of running or long-sustained swimming or diving.

The antitrochanter is small, and the inner ring of the acetabulum nearly equal in size to the outer. The ischiatic foramen is large and of a subelliptical outline. Below this, we find also an elliptical obturator foramen, which connects by a narrow strait with the long and posteriorly open obturator space.

Posteriorly, both the ilium and the ischium are drawn out into triangular points, the latter being the longer and narrower of the two. They are separated by a characteristic triangular notch, with its apex directed to the front. The ischium of *Alca torda* is comparatively a very slender bone, as shown in the figure. The part of the pubic element now generally described as the true pubis, is here but feebly developed, while the "post-pubis," as already remarked, is produced backwards far beyond the hinder extremity of the ischium to a point opposite the anterior facet of the pygostyle.

On the ventral side, the pelvis of this Auk presents us with but little worthy of long consideration, as when the bone assumes such a form as this one has, it is easy to judge of the ventral pattern of the bone from a superior view of it. In many other birds this does not hold true.

We find here that the diapophyses of that vertebra, which is opposite the isthmus of bone that divides the acetabulum from the ischiadic foramen, is the one that has been strengthened to form the *point d'appui* for the head of the former on either side.

Ventrally, a faint ridge of bone is carried down to meet the end of the diapophysis; above, the oblique muscular line, already spoken of, on the ilium is seen, while laterally the thickening of the bone supports the antitrochanter.

Of the Coccygeal Vertebræ.—(A figure giving a lateral view of the pygostyle and two ultimate caudal vertebræ of the Razor-bill will be presented in a subsequent Part.) As with nearly all the lower types of birds, the pygostyle is long and narrow, with rounded distal end, and reminds one more of the termination of a tail than this bone sometimes does.

The first six free coccygeal vertebræ are much alike, with the exception of the first one, their transverse processes are of an

equal length, rather short, and bent gently downwards. They are wider and more spreading in the anterior one, which has more the appearance of the ultimate sacral one.

The neural canal is capacious, and carried through eight of the segments, when it impinges upon the pygostyle. Above it, the neural arches and spines are well developed throughout the series.

Beneath the joints of the centra, in the median line, of the last four or five vertebræ, we find freely articulated chevron bones. These are largest posteriorly, and diminish in size as we proceed towards the pelvis—the last three joints not possessing them. They articulate by a base equally distributed between the two vertebræ; from this a stumpy process hooks forwards for a short distance.

With slight modifications for the genus, the articulations among the vertebræ of the column of *Alca torda* are exactly as we find them in other existing birds, and in the case of the caudal vertebræ, they are fully as well developed as we find them in many of the higher groups.

Of the Pectoral Arch.—In a great many of the Auks, one of the first things that forces itself upon us, after a glance at the *furcula*, is the immensely long clavicular head, which, when articulated *in situ*, is about in the same straight line with the scapula of the corresponding side. *Alca* has this feature developed most perfectly, and it seems to have been characteristic of *Plautus impennis* also. The posterior end of this clavicular head does not reach the scapula, nor a scapular process coming from the coracoid, as it does in other groups of birds. Upon the outer aspect of this long clavicular head, about its middle, there is a subcircular facet, which is placed upon a prominence developed there for that purpose, that looks nearly directly backwards. It articulates with the anterior part of the head of the coracoid, which reaches forward in a peculiar fashion to accomplish it. The arrangement in the Great Auk was similar to this, as shown by Owen's figures, and it will be seen further on that other *Alcidæ* are constructed on the same plan in this particular.

Returning to the Razor-bill, we observe that the clavicle as

it begins to curve downwards is compressed from side to side, and gradually becomes narrower from before backwards as we approach the hypocleidium. In the direction of its axis, it is moderately excavated on its outer aspect for a limited distance above. Regarding the bone from in front, we find that it is a typical U-arch, while on lateral view it curves gracefully towards the anterior border of the sternum, where an inconsiderable interval exists between the lower side of the hypocleidium and the upper edge of the carinal angle.

Nearly all the borders of the furcula in this Auk are rounded, the exceptions being the edges of the small, squarish hypocleidium, and the posterior margin of the bone a short distance from and above it.

As already described, the head of a *coracoid* is hooked forwards for the purpose of articulation with a facet on the outer side of the head of a clavicle. Below this, on the outer and posterior aspects, the bone contributes about the usual amount of two-thirds to the glenoid cavity. To the inner side of this, and perpendicular to its inferior periphery, we find the articular line of the scapular process. This latter triangular lamina of bone is perforated by a foramen, as in some other birds, just below its middle. Below the apex of this again the coracoid, with the merest apology for a shaft, immediately begins to dilate in the usual manner to support the sternal facet. In this Auk this is very large and deep from before, backward; it is slightly concave behind, very convex anteriorly. Mesiad, it is drawn out to a point, which, when both coracoids are naturally articulated, nearly meets the similar process of the bone of the opposite side. Low down on the outer margin of one of these bones a prominent lateral process is developed, which appears in other representatives of the group.

The head of a *scapula* is broad and compressed from above, downwards, slightly extending beyond the scapular process of the coracoid on the inner side, and offering the elliptical facet for the glenoid cavity on the outer.

The blade of the bone is long and much arched, the convex side being upwards. It is narrow and of nearly a uniform width from the head to the obliquely truncate posterior extremity.

I fail to find any pneumatic foramina in the bones of this pectoral arch, and do not believe that the air gains access to their cavities.

Of the Sternum.—Auks have a sternum of a style peculiar to themselves, and its pattern is well exemplified in our present subject. Although now quite characteristic, it will be seen how the form of this bone almost imperceptibly passes, by slight modifications in certain details, into the forms it assumes in several of the groups related to the *Alcidæ* (Pls. III. and IV. figs. 18 and 20).

In the Razor-bill many of its leading features can be well discerned upon a lateral view. It will be seen that its carina is a very ample plate of bone, with a gently convex border below, a protruding carinal angle in front, and a thickened anterior border above this latter, which is flattened anteriorly, and marked by a fine mesial line.

This keel is nearly as long as the body of the sternum itself, being carried backwards to a point where the true sternal body seems to terminate, but beyond this, in many water-birds, notably the divers and others, this end of the sternum is produced posteriorly, and usually symmetrically, by a thin extension of elementary bone. This ossifies to a greater or less extent and quite evenly in *Alca torda* and other *Alcinæ*, leaving in the prepared skeleton an outwardly convex posterior margin to the sternal body. My meaning will be made clearer by referring to the ventral aspect of the sternum of the Red-throated Diver, as will be seen in a figure of a subsequent Plate. We are also to observe on this lateral view of the sternum of the Razor-billed Auk, the form of the manubrium, which is of nearly a square outline, being flattened above, but with anterior and lower margins quite sharp. The coracoidal articular grooves barely meet behind at its base.

These latter are curled to the front a good deal, and are distinguished for being deep in an antero-posterior direction, but not carried out very far laterally. To the outer side of each, and situate just below a costal process, a pit-like convexity is seen with a lip of bone projecting from its lower border. A circular facet is seen within this pit to its mesial side, which is separate from the general coracoidal articulation on the

sternum, but, nevertheless, articulates with a lateral and inferior projection on the coracoid, as does the lip on its inner side just referred to, the last assisting to retain the coracoid in its articulation.

The costal processes are well developed, but not lofty, nor strikingly prominent as we find them sometimes in other birds.

Eight facets for the hæmapophyses are seen upon each of the costal borders. They face outwards, upwards, and backwards in about an equal ratio; the concavities among them seem to be devoid of pneumatic foramina, and indeed I have failed to find such apertures anywhere about this sternum, and believe it to be a non-pneumatic bone.

The distance between the anterior of these facets and the last one is less than the distance between the last one and the end of the outer xiphoidal process of the same side, although of the entire edge of this lateral border of the sternum, that part of it which may be called the costal border is nearly half of it.

The line of demarcation between the keel and the sternal body is nearly straight, and the hinder part of the latter shows but little convexity.

Viewed from in front, we are enabled to see how much the keel projects beyond the body of the sternum, and further that its inferior border is flat and nearly twice the width of the keel's own thickness, so it projects beyond the latter on both sides for its entire length.

Behind, it merges into the luniform area, already spoken of above as the mid-extension of the xiphoidal extremity.

The sternum of this Auk is 1-notched on either side, these notches being very deep, and having the form of long ellipses, with their major axes parallel to the longitudinal axis of the carina.

This arrangement evidently gives rise to a prominent xiphoidal process on each side, with their posterior ends gently deflected towards the median line.

The margins of the xiphoidal notches and processes are thickened to increase their strength, a thickening which is carried up some distance on the lateral borders of the sternum.

But one prominent muscular line is to be observed upon this aspect, and it is continuous with other bounding lines of the bone. Tracing them as one line, we must commence for either side at the junction of the coracoidal grooves behind the manubrium, a line then bounds the inferior margin of the coracoidal articulation, to pass over the process described at the lower border of the pit below the costal process, whence it passes to the lower edge of a prominent and projecting ledge of bone that supports the hæmapophysial facets. Including this part and on it may be considered as the true pectoral line. Opposite the third facet from the last, it appears to be deflected inwards, but in reality the lateral border of the sternum leaves the costal edge at this point. Between the ultimate facet and the one beyond, the line really changes its course, running on the surface of the sternal body, nearly parallel with its lateral border, to pass close along the inner edge of the xiphoidal notch, to terminate at the apex of the luniform area of that side.

This pectoral line is well worthy of one's attention, and it is my intention to compare it and its modifications in other forms as we come to the consideration of this aspect of the sternum.

As already stated, the convexity of the hinder half of the sternum is not very great, while anteriorly it is quite moderate, and the narrowness of the bone over its unusual length in proportion, makes it appear even less than it really is.

On its thoracic aspect the sternum is smooth and bears outall that we have said above in regard to its form. An exceedingly shallow groove is found in the median line over the keel, otherwise this view offers us nothing that requires special mention, beyond the points I have already called attention to elsewhere.

Plautus impennis had a long and narrow sternum which was sometimes devoid both of notches and foramina in its xiphoidal extremity. Owen gives two figures of this bone (figs. 1 and 2) in his memoir upon the osteology of this extinct Auk, a ventral and an anterior view. The lateral aspect of it may also be seen in the same monograph in the full skeleton of the bird. I think in the figure showing the under view, the keel should be drawn so as to project beyond the sternal body, as it does in most Auks,

and Owen's own lateral view of the bone shows that it would if a direct ventral view had been presented by the author.

I have copied, life-size, the posterior end of this bone from the figure in question, and present it here in fig. 9, Pl. II., to show how in his specimen there was a total absence of notches and foramina, but we now know that that was not invariably the case, except perhaps in very old individuals.

Of the Pectoral Limb.—Air does not gain access to the cavities of any of the bones of the skeleton of the pectoral limb in *Alca torda*, and this seems to be the case with the majority of the more lowly organised forms of birds.

The limb, however, is ample, and in other particulars well developed and proportioned. The bones in the specimen before me yield the following measurements:—The humerus is 7·3 centimetres long; the ulna, 5·7; the radius, 5·4; the carpo-metacarpus, 3·7; the pollex phalanx, 1·7; the proximal phalanx of index, 1·9; its distal one, 2·1; and the small phalanx of middle digit, 0·9 centimetres long.

The two usual carpal bones are present, but I believe my specimen lacks at least one or two sesamoids that are found at the elbow in most Auks; it has but one of these present, and I will defer their description as found in the *Alcidæ* until we come to the Puffins and other forms further on, where my material will permit me to enter upon the subject more thoroughly.

The *humerus* of the Razor-bill Auk seems to agree in all essential particulars with the same bone in the limb of *Plautus impennis* as figured for us by Professor Owen in the memoir I have quoted above. This eminent anatomist also says in his *Anatomy of Vertebrates* that "A section of the humerus of the Penguin shows it to be solid, that of the Auk (*Alca*) shows a small medullary cavity with dense and rather thick walls." This is the case in *Alca torda* also, and the bone is proportionately heavy in consequence. In a plate which is to follow in another Part, I present the humerus as it is found in several birds in which it was advisable to compare it. Among these, a figure represents the palmar aspect of the humerus of the Auk we have in hand.

Holding the humerus in such a position that the radial crest is towards you, we notice but little curvature in the shaft: turn-

ing it quarter way round, however, until we have a palmar aspect presented, the sigmoid curve observable in others of the class becomes evident, though here it is largely due to the positions of the ends of the bone, and not so much to the slight curvature which the shaft presents alone.

The humeral head curls gently anconad, and has the form of a hemi-ellipsoid with its convex surface, as usual an articular one for the glenoid cavity. Between it and the ulnar crest a wide notch occurs, which is continuous with the concavity beneath the curling head. The ulnar crest overhangs a deep pit, the site for pneumatic foramina in those birds where they occur, and both project well away from the shaft of the bone. The radial crest is low and gently convex throughout. It is bent palmad, while its anconal surface is continuous with the side of the shaft upon that aspect.

Upon the anconal side of this end of the shaft, the tuberosity for the middle pectoral muscle is strongly developed, this being the muscle that extends for nearly the entire length of the sternum of this Auk as shown by the pectoral line which I described in detail when upon the description of the ventral aspect of the sternum above. It is seen also in other Auks, as well as in the Penguins and Gulls.

The shaft being considerably compressed is quite flat; one rounded edge dividing the two surfaces extending in continuation with the radial crest to the ectocondyloid tubercle, the other from the surface beneath the overhanging humeral head to a point on the opposite side to the ulnar tubercle at the distal extremity.

The nutrient foramen pierces the shaft at the junction of upper and middle thirds on the lower side of the palmar aspect. At the distal extremity we find the grooves for the passage of tendons deeply sculpt at the termination of that surface which is continuous with the anconal side of the radial crest of the proximal end of the bone.

Opposite these grooves upon the other surface we find the oblique and ulnar tubercles, which are here prominently projecting from the distal end of the humeral shaft. Above the former the "ectocondyloid tubercle" stands out upon the border dividing the two surfaces of the shaft. It is near enough

to the proximal end of the oblique tubercle to have it appear that they are separated from each other by an intervening valley.

Owing to the way these parts are fashioned at the distal end of this humerus, it has the appearance as though it had been squarely cut across, and the oblique tubercle allowed to project below. This can better be appreciated by a glance at the figure of the bone.

With the skeleton of the pectoral limb closed in a position of rest, we notice that both the *ulna* and *radius* are flattened, and that in a plane nearly at right angles to the one which the flattened surfaces of the humeral shaft are at right angles to; or to better express the condition, and more accurately, we might say, that if the plane in which either of the flat shaft surfaces of the humerus is found was produced upwards, the limb being in the position indicated, it would cut the upwardly produced plane of the surfaces of the radius and ulna at some little distance *above* the three bones, making a wide obtuse angle.

The interosseous space between the radius and ulna is quite wide and spindle-form in outline, the bones nowhere touching each other except at their distal and proximal extremities.

The head of the *radius* is fashioned upon the same plan as in birds generally; its neck is cylindrical, but all beyond is compressed and flattened as just described. The radial shaft is nearly straight, being but slightly concave towards the ulnar side. Its distal extremity articulates with the usual bone of the carpus, and two strong tendinal grooves which mark it here are continued directly on to the latter to extend as far as the head of the carpo-metacarpus.

An olecranon of no mean size is to be seen at its usual site upon the *ulna.* Upon the radial side it is separated from a prominent sub-compressed process, against which the head of the radius articulates, by a longitudinal excavation, which in the living Auk harbours the extensor tendons. The deep articulatory cup at this end of the ulna, for the tubercle on the humerus, is supported on a somewhat elevated base, differing in this respect from others of the class.

The shaft of this bone is moderately bowed outwards, and

along this aspect a feebly developed row of quill-knobs are to be discerned. Its distal extremity is modified for the usual articulations with the overlapping end of radius and both of the carpal segments.

These latter have the same general form as we find that they assume among other birds, with their articular facets opposed to the surrounding bones in a manner common to the majority of the class.

Special attention is invited to the form of the first metacarpal bone of the carpo-metacarpus, as further on its comparison with the same part in other water-birds will be particularly attended to. Here it is seen to be quite long, without special processes, in fact an elongated piece of bone parallel with the shaft of index metacarpal, and anchylosed with it for its entire opposed length. True to the common type of the avian manus, the index metacarpal constitutes the main shaft of this composite segment. *Alca torda* has it very straight throughout its length, and is entirely devoid of the compression to flatness so characteristic of the long bones of the brachium and antibrachium. On the contrary, it is more nearly cylindrical than we are always accustomed to find it. Slender and slightly bowed, the last metacarpal of manus is a simple ribbon of bone, devoid of any processes, and fast only by its upper and distal ends, its concave aspect being directed towards the index metacarpal.

Pollex phalanx is a long, pointed, and subtrihedral joint, with slightly enlarged distal end, but with no evidence of a second phalanx being borne upon it, nor a claw.

The proximal phalanx of index digit has its blade-like portion quite narrow, solid, and unperforated by foramina as in the Gulls and some other birds. Its hinder border is convex and terminates distally in a prominent little process, which I find in Marsh's figure of the extinct *Ichthyornis victor*.

Further on we will see that this is not present in all water-birds, but appears to be in most Auks. Owen represents it as a feature of this phalanx in *Plautus impennis*. A lamelliform, quadrilateral process also projects from the anconal side of the antero-distal aspect of this phalanx, that seems to be intended to guide the tendons to the ultimate joint. However this may

be, a like process is found similarly situate upon the index metacarpal.

The last phalanx of this digit is longer than the single one in the pollex; it is flattened antero-posteriorly, and, like the joint of the thumb, is without a claw or another joint beyond.

Almost spine-like in its form and dimensions, the single phalanx of the last or middle metacarpal is very nearly as long as the half of the first phalanx of the index digit.

Penguins have both their metacarpal and phalangeal bones flattened as the bones of their antibrachium are, and as we found the latter to be in our present subject.

Parker also tells us that "in the Penguins the pollex has two phalanges, and its metacarpal bone (which is distinct in the young birds) ankyloses with that of the second digit. The third metacarpal is slender and straight. The bones of the manus are singularly elongated and flattened" (*Ency. Brit.*, 9th ed., art. "Birds"), so that in these birds a very different condition of the skeletal parts of the manus exists. Whereas in *Plautus impennis* they agree almost entirely with the parts as I have just described them for *Alca torda.*

Of the Pelvic Limb.—Pneumaticity of the skeleton of the limbs, I believe, always commences with the proximal segments; so that if the humerus or femur is found to be non-pneumatic, we may rest assured that the bones of antibrachium and pinion, and those of scelos and pes, are also so. Then again, my observations lead me to think that of the two bones, humerus and femur, if either are found to be pneumatic in the skeleton of a bird, it is pretty sure to be the former.

Careful examination of the femur of *Alca torda* convinces me that it is a completely non-pneumatic bone, as are the bones of the remainder of the skeleton of this limb.

Measurements taken as in the case of the pectoral extremity yield the following results:—the femur is 4 centimetres long; the tibia, 7·2; the fibula, 4·3; the tarso-metatarsus, 3·1. In measuring the toes I will give their lengths all in the same order to avoid repetition, beginning with the proximal phalanx and ending with the bone of the claw or ungual phalanx. This latter will be measured by taking its longest chord.

Further on it will be seen that I have good reason to suspect

at least a rudimentary first metatarsal in this Auk; but my specimen exhibits no such bone, and its discussion will be taken up in some of the other forms.

The first phalanx of the second toe measures 1·4 centimetre; the next, 1·35; the claw, 0·65. In the third or middle toe these joints stand: proximal, 1·55; next, 1·2; next, 1·1; claw, 0·65.

Five joints allotted to the fourth or inside toe measure respectively: proximal, 1·2 centimetre long; next, 0·95; next, 0·85; next, 0·9; and the claw, 0·50.

Sir Richard Owen in his osteology of the Great Auk presents in his plates several figures of the bones of the pelvic limb of that bird. Of these, I have reproduced in my Plate V. the femur and the tibia and fibula; and in order to compare them with the corresponding bones in the Razor-bill Auk, I have drawn the latter in the same positions as those chosen by that eminent anatomist for *Plautus*.

In the *femur* of *Alca torda* the axis of the neck makes an obtuse angle with the axis of the shaft below. Its head is globular, and the smooth articular surface is continued on to the summit of the bone to occupy the entire area of that part, terminating along the very low trochanterian ridge, which bounds it outwardly. Scarcely any excavation is made at all for the ligamentum teres on the superior and inner aspect of this globular head. Many birds have this quite deep, and a noticeable feature of this end of the bone.

The trochanterian ridge is produced some little distance down the shaft, while the outer surface of this great trochanter is roughened for muscular insertion.

There is no trochanter minor present in this Auk, and the only birds in which Owen found it were the extinct *Aptornis* and *Dinornis*. Marsh does not mention it as occurring in any of the extinct toothed birds of the Cretaceous beds of the United States.

The shaft of the femur in the present subject is subcylindrical and but slightly bent in an anterior direction. Inwardly it contains a large medullary cavity, while externally it is smooth and fairly shows the lines of muscular markings.

Of the two condyles the external one descends the lower, the bone being held in the vertical position. This one also projects

the further posteriorly, and is as usual cleft from above downwards in order to articulate with the head of the fibula. Anteriorly, the "rotular channel" does not extend very high up on the shaft, and the vertical crests of the condyles are prominent upon this aspect.

Behind, the "popliteal depression" is well excavated, and is divided by a low transverse ridge from the well-marked intercondyloid fossa. Tubercles for ligamentous insertion are to be found at their usual sites, and the medullary orifice is seen on the posterior aspect of the shaft at the junction of middle and upper thirds.

I find no *patella* in this Auk, and it may have been lost, although from the form of the proximal extremity of tibia I am rather inclined to believe that it does not possess one. Owen does not figure one for *Plautus impennis*, and probably it also lacked it. Penguins have a very large patella, as seen in my figure of this sesamoid for *Aptenodytes pennantii*, in the seventh volume of the *Proceedings of the United States National Museum*, page 326, where other forms are also compared and figured. Should a patella be found in *Alca torda*, no doubt it will occupy much the same position as it does in *Podiceps*, another form which possesses a lofty cnemial process, as well as having a large patella.

Upon the summit of the *tibia* we find the usual undulatory articular surface, pitted and elevated to receive the condyles of the femur. A bold rotular process is reared above this, with pointed apex, and bearing the pro- and ecto-cnemial ridges upon its anterior margins, which very soon, however, merge into the shaft below (Pl. V. fig. 26). The shaft is smooth and straight, being subelliptical on transverse section for nearly its entire length, and is spanned directly across just above the condyles, anteriorly, by the tendinal bridge of bone for the confinement of the extensor tendons. At its outer side above, the fibular ridge is developed, extending for no great distance down the tibial shaft, parallel to its long axis.

The distal condyles are separated from each other by a deep intercondyloid fossa in front, which, as it passes round behind, becomes wider and shallower. This form is influenced by the shape of the condyles themselves, which are found to be pro-

minent and thick in front, where the major share of the articular surface is, to become thin and almost insignificant ridges behind.

As with most birds the lateral aspect of either one shows it to be of a reniform outline, with the convex surface below for the tarso-metatarsal head.

A prominent tubercle is found upon this lateral aspect of the inner condyle, which I have described as being a tolerably constant feature in many other birds.

Very delicate in its proportions, the *fibula* is seen to anchylose with the tibial shaft at this junction of its middle and lower thirds. It is firmly attached to the fibular ridge of its companion bone by a dense fibrous ligament.

The tubercle for the insertion of the tendon of the biceps muscle is situate low down, being below the middle of this tibio-fibular articulation. At the lateral aspect of the fibular head above, this tendon grooves the bone in a vertical direction; the anterior part of the groove also affording room for insertion of the external lateral ligament.

The articular area at the summit of this bone is of a quadrilateral form, with the long axis in the antero-posterior direction; when articulated, as in life, with the tibia, the fibular head is situated rather the more posterior of the two, and below the plane of the articular summit of the larger bone.

Transverse sections made anywhere through the major part of the shaft of the *tarso-metatarsus*, yield a parallelogramic figure.

This is particularly true of the middle third of the bone, where all the sides are flat; the wider and nearly equal anterior and posterior ones being at right angles to the narrower and nearly equal lateral ones. The salient angles are sharp and well defined, those behind having their vertical lines running on either side, between the outer and inner margins of the hypotarsus and the posterior edge of the inner and outer trochlea; those in front being coincident with the anterior edges of these trochleæ, and carried vertically upwards on either side to mid-points of the anterior peripheries of the deep articular concavities found at the summit of the bone. These latter are divided on the border mentioned by a prominent

rounded tubercle, which, when the limb is articulated, passes between the condyles of the tibia.

The hypotarsus, though broad, is on the whole rather feebly developed. It is vertically grooved by tendinal canals, which remain open in this Auk. The upper part of the shaft, anteriorly, is excavated and pierced in the usual manner by the two foramina, which here occur as in most birds, opening on either side of the hypotarsus behind.

Distally, the tarso-metatarsus of *Alca torda* presents three trochleæ for the proximal phalanges of the toes. Of these, the inner one is by far the most elevated, as well as most posterior (figs. 28, 30, Pl. V.).

Next, in both these respects, comes the outer trochlea; the lowest and most anterior being the middle one. These trochleæ are strongly grooved longitudinally, this being best marked on the middle one, next best on the outer one, and rather faintly on the inner trochlea.

These grooves pass all the way round to the commencement of their posterior bases.

The end of this bone is pierced by the usual arterial foramen in the crease between the bases of mid and outer trochleæ, it making its appearance behind at the bottom of quite a concavity which is there found, just above the trochlear protuberances. *Plautus impennis* had this bone fashioned very much upon the same plan as I have described it for the Razorbill Auk. Some interesting modifications of it, however, will be noticed as we pass to the higher groups, through the Puffins and *Laridæ*.

Taken in connection with the measurements I have already given, the figure of the skeleton of the foot of this Auk will convey a clearer impression of its appearance and parts than any verbal account that could be rendered (Pl. V fig. 28). It will be seen that the toe-joints are arranged upon the most common plan of the avian foot, and in very even proportion as to lengths and calibre. By the construction of their anterior and posterior trochlear ends, the action of any of these toes is limited to one plane.

The claws or ungual phalanges have the tubercle at the under sides of their proximal ends, equal, in each instance, to half

the length of the claw. The inner and outer aspects of these terminal phalanges are also grooved to their very tips, affording lodgment to the minute phalangeal branches of the plantar artery and vein which lie in them, and thus pass beneath their horny encasements to their apical extremities.

Summary of the Principal Osteological Characters of Alca torda.

(A few negative characters are included.)

1. Superior mandible hooked at its extremity; anterior half laterally compressed, and culmen raised in a convex prominence above the posterior half.

2. Nostrils large, long, and subelliptical; pervious, no internasial osseous septum. Nasal bones are schizorhinal.

3. Large superorbital glandular depressions, separated by thin, osseous, longitudinal crest; a constant foramen of some size at their anterior ends.

4. Crotaphyte fossæ largely developed, do not meet in the median line by a small median interval, separated from the supraoccipital area by a prominent crest.

5. Os uncinatum present; lacrymal bone articulates with nasal and frontal, and anchyloses below with pars plana.

6. Anterior portion of the summit of the ethmoid divided transversely under the cranio-facial hinge.

7. Interorbital septum contains one large, quadrilateral vacuity; track of olfactory nerves fail to be separated by bone to a greater or less extent; bony deficiency in the neighbouring wall of the brain case. Foramen rotundum distinct, or may merge only with the small nerve foramina in its immediate neighbourhood.

8. Maxillo-palatines composed of compact bony tissue, subcircular in outline, concavo-convex in form, do not meet each other or the vomer, but anchylose anteriorly with premaxillary (dentary process), nasal and palatine.

9. Vomer in the adult indistinguishably united behind with the palatines, median carination beneath and grooved above, anterior extremity obliquely truncated so as to produce a median apex in which the sides of the groove and keel meet.

10. The palatines are continuous with and anchylosed to the

dentary processes of the premaxillary in front, being separated by a considerable interval. Postero-external angles rounded, and in contact for their entire lengths beneath the rostrum.

11. Rostrum pointed anteriorly and lying in the vomerine groove, slender posteriorly.

12. Pterygoids touch each other in front, and the closely opposed palatine heads, riding the rostrum. Basi-pterygoid processes absent.

13. In the mandible we find the surangular with a large elliptical foramen through it, but the usual vacuity between the forks of the dentary on one hand, and the surangular and angular on the other, closed in by the splenial. Mandibular angle recurved.[1]

14. There are forty-four vertebræ in the column, besides a pygostyle, that probably contains several more. First pair of free ribs are attached to the fourteenth; first pair that reach the sternum by costal ribs are from the sixteenth vertebra. At least six ultimate vertebræ of the dorsal series are opisthocœlous. The twenty-third is the first that is appropriated by anchylosis with the sacrum, which latter has fourteen in all. Eight free caudal vertebræ exist.

15. Unciform appendages free, costal and vertebral ribs slender and long, the ultimate ones being carried as far back as the sixth caudal vertebra.

16. Sternum long and narrow, deeply 1-notched, manubrium wedge-shaped, angle of carina very prominent.

17. Pectoral arch well developed, *scapula* long, narrow, and distally truncate; head of *coracoid* overlaps clavicle, its scapular process perforated by a foramen, but does not reach clavicle. *Clavicles* U-shaped; head very long, with raised facet on outside for head of coracoid, small hypocleidium present, though much arched in that direction, the furcula does not reach the sternum by quite an interval.

[1] Huxley in his Classification of Birds (*Proc. Zool. Soc.*, 11th April 1867) places the *Laridæ*, the *Procellariidæ*, the *Colymbidæ*, and the *Alcidæ*, all in his group *Cecomorphæ*. Among the few distinguishing osteological characters presented is the one which says that "the angle of the mandible is not recurved." As a representative of the *Alcidæ*, this certainly does not apply to *Alca torda*, in which Auk the angles of the mandible are very decidedly recurved. It is still more evident in the Puffins and some other forms.

18. *Pelvis* long and narrow; ilio-neural grooves instead of canals; preacetabular area far in excess of postacetabular; double row of foramina on dorsal aspect between diapophyses of six or seven sacral vertebræ. Post-pubis long, slender, and far produced behind. Triangular notch between ilium and ischium on posterior border, these elements here being drawn out in pointed extensions. Ischiac foramen large and separate. Obturator foramen opens into obturator space.

19. Pectoral limb non-pneumatic but of good proportions and development. Humerus with large head, low radial crest, flat shaft, and ectocondyloid process present. Radius and ulna with flattened shafts. Two bones in carpus. First metacarpal bone parallel with that of index and anchylosed to it for the entire length of foramen. One phalanx in pollex, two in index, and one in middle or last digit.

20. Pelvic limb non-pneumatic, well-proportioned and of good development. Axis of neck of *femur* makes an obtuse angle with axis of lower part of shaft. Shaft cylindrical. Excavation for round ligament very shallow, and small outer condyle the lower. Shaft of *tibia* straight and subelliptical on section. Cnemial process, bearing pro- and ecto-cnemial ridges, prominent and carried well above summit of shaft. Bony tendinal bridge present at distal end. *Fibula* long and slender, lower end anchyloses with tibial shaft. The *tarso-metatarsus* has a grooved and flattened hypotarsus. Shaft quadrilateral on section. The inside trochlea the highest and most posterior, the outside one next, and the middle one the lowest and most anterior. Three anterior toes with three, four, and five joints respectively, all justly proportioned. Ungual phalanges laterally compressed, slightly curved, and inferior basal tubercle half as long as claw.

Supplementary Notes on the Skeleton of the Great Auk.

As I have remarked in the forepart of this paper, I have at hand two fairly complete skeletons of this now probably extinct alcine form. They were kindly loaned me by Mr F. A. Lucas, the osteologist of the United States National Museum at Washington. Mr Lucas, I understand, intends to fully describe these skeletons, which he recently discovered, so I will only say here that upon examining the *skull*, I find it to agree in the main with Owen's de-

scription of it; a series of them, however, will show that they differ in the number and size of the foraminal perforations in the supra-orbital glandular depressions; in the width of the crest dividing the crotaphyte fossæ in the median line of the parietal region; in the fact whether or not the median supraoccipital eminence be perforated by one or two foramina, or whether it be unperforated. In a great many respects the skull of the Great Auk resembles the skull in *Alca torda*, and undoubtedly both forms spring from precisely the same stock, and structurally are quite closely affined, *Plautus* being much the more ancient type, while *Alca* represents a modern form of Auk. Owen we know figured the xiphoidal end of the sternum of the Great Auk entire, but these skeletons go to prove that that bone was either entire, or may be showing a fenestra on both sides, or only upon one side, or on one side and notched upon the other, or finally notched upon both sides. This, I am inclined to believe, may have depended entirely upon the age of the individual. Mr Lucas further sent me quite a large variety of the long bones of this Auk, in order to show how much they varied in length; this, too, undoubtedly is due to age, as the smaller bones, in many instances, show evident signs of having belonged to immature specimens. The *furcula* is of a typical alcine pattern, and agrees in all particulars with that bone as figured by Sir Richard Owen in his classical memoir upon *Plautus impennis*.

There are twenty-two vertebræ in the spinal column sent me, before we come to the pelvis, which latter bone, strange to say, was more apt to be broken, and more difficult to find, being apparently fewer of them, than any other of the skeleton, so I am told, by Mr Lucas, who, as I have said, enjoyed the rare privilege of exhuming so many of these remains, at a date as late as 1887, from a locality where these interesting alcine types once abounded and lived in security.

EXPLANATION OF PLATES I.–V.

[*Note.*—Some of the figures here given are not described in the present paper, while others that are described do not appear, but will be presented in a subsequent Part. One of my aims in doing this has been to allow me the opportunity of placing side by side in the Plates, bones which I wished to have *directly* compared in that way.]

Plate I.

Fig. 1. Skull of *Alca torda*, right lateral view; life size.

Fig. 2. Mandible of *Alca torda*, viewed from above; life size; same specimen as fig. 1.

Fig. 3. Skull of *Alca torda*, basal view; life size, and mandible removed.

Fig. 4. Skull of *Alca torda*, superior view, mandible removed; life size. These four figures were drawn by the author from a fine skeleton of this Auk, presented him by the late W. A. Forbes, B.A., at the time he was Prosector to the Zoological Society of London.

Plate II.

Fig. 5. Skull of *Alca torda*, posterior view; mandible removed; life size. From same specimen shown in Plate I.

Fig. 6. Skull of *Larus delawarensis*, posterior view; mandible removed; life size. Drawn by the author from a specimen in his own collection.

Fig. 7. Skull of *Urinator lumme*, posterior view; mandible removed; life size; by the author, from specimen 16,628 of the collection in the Smithsonian Institution.

Fig. 8. Skull of *Fulmarus glacialis rodgersii*, posterior view; mandible removed; life size; by the author, from specimen 12,613 of the collection in the Smithsonian Institution.

Fig. 9. The xiphoidal extremity of the sternum of *Plautus impennis*, pectoral aspect; by the author, after Sir Richard Owen's drawing.

Fig. 10. Skull of *Charadrius dominicus*, posterior view; mandible removed; life size; by the author, from specimen 16,715 of the collection in the Smithsonian Institution.

Fig. 11. Skull of *Hœmatopus backmani*, posterior view; mandible removed; life size; by the author, from specimen 13,636 of the Smithsonian Collection.

Fig. 12. Skull of *Larus philadelphia*, posterior view; mandible removed; life size; by the author, from a specimen in his own collection.

Fig. 13. Skull of *Chionis minor*, posterior view; mandible removed; life size; by the author, from specimen 16,950 of the collection in the Smithsonian Institution (type of Kidder's *Memoir on the Osteology of Chionis*).

Plate III.

Fig. 14. Skull of *Hœmatopus backmani*, left lateral view; life size.

Fig. 15. Mandible of *Hœmatopus backmani*, viewed from above; life size.

Fig. 16. Skull of *Hœmatopus backmani*, superior aspect; life size; mandible removed.

Fig. 17. Skull of *Hœmatopus backmani*, basal view; mandible removed; life size.

Figs. 14, 15, 16, and 17 are all drawn by the author from the skeleton of the same individual (No. 13,636 of the Smithsonian Collection).

Fig. 18. Sternum of *Alca torda*, right lateral view; life size; by the author, from a specimen presented him by Mr Forbes (see figs. 1, 2, 3, and others).

PLATE IV.

Fig. 19. First dorsal vertebra of *Urinator lumme*, with its pair of ribs, the latter with their epipleural appendages; all articulated *in situ;* posterior view; life size; by the author, from specimen 16,628 of the collection in the Smithsonian Institution.

Fig. 20. Sternum of *Alca torda*, pectoral aspect; life size; same specimen as in fig. 18.

Fig. 21. Sternum of *Larus delawarensis*, pectoral aspect; life size; by the author, from a specimen in his own collection.

Fig. 22. Sternum of *Hæmatopus backmani*, pectoral aspect; life size (specimen 13,636 of the Smithsonian Collection).

Fig. 23. Sternum of *Chionis minor*, pectoral aspect; life size (Kidder's type specimen). All the drawings in this plate by the author.

PLATE V.

Fig. 24. Right tibia and fibula of *Plautus impennis;* life size; by the author, after Owen.

Fig. 25. Right femur of *Plautus impennis*, anterior surface; life size; by the author, after Owen.

Fig. 26. Right tibia and fibula of *Alca torda;* life size, showing same surfaces as the bone in fig. 24; by the author, from the specimen presented him by Mr Forbes.

Fig. 27. Right femur of *Alca torda*, anterior surface; life size; from same specimen as fig. 26.

Fig. 28. Skeleton of right pes of *Alca torda*, anterior aspect; life size; by the author, from same specimen as in fig. 26.

Fig. 29. Direct view from above of the tarso-metatarsus, proximal extremity; life size; from the bone shown in fig. 28.

Fig. 30. Direct view from below of the tarso-metatarsus, distal extremity; life size; from the bone shown in fig. 28.

Fig. 31. Vomer of *Alca torda*, inferior surface; life size; by the author, from the skull shown in Plate I.

Fig. 32. Cervical vertebræ, first to the seventh inclusive, of *Urinator lumme*, right lateral view; life size; by the author, from specimen 16,628 of the collection in the Smithsonian Institution.

Fig. 33. Vomer of *Recurvirostra avocetta* (after Garrod).

Fig. 34. Vomer of *Chionis alba* (after Garrod).

Fig. 35. Vomer of *Hæmatopus ostralegus* (after Garrod).

Fig. 36. Vomer of *Numenius arquatus* (after Garrod).

Fig. 37. Hyoid arches of *Larus delawarensis;* life size, from below; by the author, from a specimen in his own collection.

Fig. 38. Vomer of *Larus delawarensis*, from the same specimen shown in fig. 37.

Fig. 39. Hyoid arches of *Chionis minor;* life size, from below; missing parts in dotted lines. By the author, from Kidder's type specimen (No. 16,950, Smithsonian Institution Collection).

Fig. 40. Vomer of *Sterna hirundo* (after Garrod).

ON THE EFFECT OF CHRONIC DISEASE OF THE VALVES OF THE HEART UPON THE SOUND ORIFICES, THE CAVITIES, AND THE WALLS.

By D. J. Hamilton, M.B., F.R.C.S.E., F.R.S.E., *Professor of Pathology, University of Aberdeen.*

Introductory.

The relationship of the condition of the walls and cavities of the heart to that of its apertures altered by disease, is admittedly of the greatest prognostic importance. The doctrines current on the subject, however, are somewhat loose and untrustworthy. Thus the various degrees of incompetence and constriction of the aortic are roughly held to occasion more or less hypertrophy of the left ventricle, but whether one form of lesion occasions it more than another—whether, for example, simple incompetence, incompetence with constriction, or incompetence with dilatation, &c., is attended with the greatest amount of hypertrophy—and what the mechanism is by which the difference, if any, is to be accounted for, seem to be insufficiently understood The effects of a lesion of one orifice upon the size and competence of the others, is also a matter which might well be placed in a clearer light. The mechanism of cardiac dilatation, moreover, appears to be worthy of further investigation.

This paper has been written chiefly with the object of supplying some of the facts which have hitherto been needed to place the pathology of hypertrophy and dilatation upon a firmer footing. For the last thirteen years I have kept an accurate record of the size of the apertures, the thickness of the walls, the length of the ventricular cavities, the weight of the organ, &c., in nearly every *cadaver* which has passed under my notice as pathologist to the Edinburgh and Aberdeen Royal Infirmaries. The facts derived therefrom have mainly served as the basis of the conclusions I have drawn in the sequel.

The measurements of the orifices were all made by carefully-graduated box-wood cones. These are undoubtedly much the

most reliable means of ascertaining the size of any aperture in the body, provided they be judiciously used. The cone should be introduced into the aperture in the same direction as that in which the blood naturally passes through it. It should be pushed through just until it catches, but no violence should be employed to drive it beyond this. It will be found that a graduation to decimals of an inch diameter is a sufficiently fine subdivision. The weights were taken in ounces avoirdupois.

The estimation of the size of the ventricles was arrived at by measuring *the distance from the apex of the cavity up to the base of the nearest sigmoid segment.* I am well aware that this method of ascertaining the size of the ventricle might be held to be open to objection. As a matter of experience, however, it will be found that it gives a much more accurate estimate of the total capacity of the cavity than might at first be supposed, and when combined with a description of the general appearance of the organ, must be held to be infinitely preferable to an unsupported and general statement.

The measurement of the walls was always taken at their thinnest and at their thickest parts; the sub-pericardial fat was not included, and the parts selected were those intervening between the musculi papillares.

The figures which are quoted in the paper are, of course, the *averages* of the cases observed under any particular class.

Weights and Measurements of the Normal Heart.

In estimating the weight and dimensions of any organ, it is necessary to draw conclusions only *from absolutely healthy individuals, who have met their death suddenly by accident.* In no organ must this be more rigidly enforced than in the case of the heart. In order to be exact, we must also have some general notion of the bulk of the individual as derived from the height and girth at the shoulders, and, of course, sex must be taken into the reckoning. It is also essential to be informed of how much of the vessels in the case of the heart was left attached, and whether the heart was weighed before or after emptying it.[1]

[1] The discrepancies to be found in the figures given by Peacock, Glendinning, Bizot, Rosenstein, and others are probably owing to failure in the observance of these precautions.

The following statistics were derived from the examination of 27 males and of 4 females, all over 19 years of age, who were in perfect health at the time of death, and who were accidentally killed. The heart was excised in all cases by cutting through the middle of the arch of the aorta and through the pulmonary artery close to the bifurcation. The attached parts of the vessels were included in the weights, and the organ was invariably opened and washed out before the weight was ascertained.

My results show briefly that the commonest *weight* of the male heart, excised as before mentioned, was from 12 to 13 oz., and that it ranged between 10 and 16 oz. They also demonstrate that the heaviest average of hearts was in the tallest individuals, although there were exceptions to this rule, and that the heart, although generally, was not invariably of low weight in persons of small stature.

In the female the organ usually weighed between 10 and 11 oz. It ranged from 7 to 15½ oz.

The *diameters of the various orifices* were found to be as stated in the accompanying table:—

Diams. of Orifices—Male.

	Greatest.	Least.	Average.
Aortic,	1·3 in.	·9 in.	1 in.
Mitral,	1·8 „	1·1 „	1·4 „
Pulm. Art.,	1·5 „	1 „	1·2 „
Tricuspid,	2·2 „	1·3 „	1·8 „

Diams. of Orifices—Female.

	Greatest.	Least.	Average.
Aortic,	1 in.	·8 in.	·9 in.
Mitral,	1·5 „	1 „	1·2 „
Pulm. Art.,	1·3 „	1 „	1·1 „
Tricuspid,	1·7 „	1·4 „	1·5 „

My statistics also show that the taller the subject the larger the orifices, but that there were exceptions to this rule. When one of the orifices was large, the others were usually found to be correspondingly so.

The measurement of the *ventricular cavities* in the foregoing healthy hearts, estimated from the fixed points before

mentioned, showed that in the male, the lowest for the left ventricle was $2\frac{1}{2}$ in., the highest $3\frac{3}{4}$ in., and the average $3\frac{1}{4}$ in.; while in the female, the lowest was $2\frac{1}{4}$ in., the highest $3\frac{1}{2}$ in., with an average of 3 in.

That of the right ventricle in the male ranged between 3 and 4 in., with an average of $3\frac{3}{8}$ in.; while in the female it lay between 3 and $3\frac{1}{4}$ in., with an average of $3\frac{1}{16}$ in.

The *thickness of the wall of the left ventricle* was, as a rule, found to be about $\frac{1}{4}$ in. at its thinnest and $\frac{1}{2}$ in. at its thickest, both in the male and female; while that of *the right ventricle* was on an average $\frac{1}{8}$ in. all over in both sexes. Parts of it occasionally measured as much as $\frac{1}{4}$ in. or as little as $\frac{1}{16}$ in.

As the statistics which I give of diseased hearts include both males and females, it will be necessary to frame an approximate statement of the weights and measurements for comparison. The following is founded on the different averages just given for both sexes.

Table of Average Weight and Measurements of the Normal Heart.

Weight 10 to 13 oz.

Diams. of Orifices.		Cavities and Walls.	
Aortic,	·9 to 1 in.	L. Vent.,	3 to $3\frac{1}{4}$ in.
Mitral,	1·2 „ 1·4 „	Wall $\frac{1}{4}$ in. (at thinnest) to $\frac{1}{2}$ in. (at thickest).	
Pulm. Art.,	1·1 „ 1·2 „	R. Vent.,	$3\frac{1}{16}$ to $3\frac{3}{8}$ in.
Tricuspid,	1·5 „ 1·8 „	Wall,	$\frac{1}{8}$ in. (all over).

It should be mentioned that the weights and measurements of the diseased hearts were all estimated on the same conditions as in the case of those which were healthy.

Effects of Chronic Disease of One Orifice upon the Size of the Others.

The general impression is that chronic disease of one orifice in course of time has a detrimental effect upon the size and competency of the others. Balfour,[1] for instance, holds that the most frequent cause of serious tricuspid regurgita-

[1] *Diseases of Heart and Aorta*, 1876, p. 181.

tion is mitral stenosis, and that great obstruction at the aortic orifice has a similar effect. The blood is hindered in its passage onwards, and hence tends to regurgitate upon the right side of the heart. On the other hand, he says that aortic regurgitation, although a frequent enough disease, is anticipated in its injurious results on the other orifices by its own peculiar sources of mortality, and hence it is only comparatively rarely that aortic regurgitation gives rise to tricuspid regurgitation of a serious character.

It remains to be seen in how far this notion is borne out by facts.

A. *Pure Aortic.*

(1) Aortic of normal size, but incompetent.

In this case the average size of the various orifices was the following :—

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
·99 in.	1·3 in.	1·1 in.	1·8 in.

It would thus seem that in simple regurgitant aortic without alteration in the size of the orifice, the effect upon the size of the other orifices is practically *nil.*

(2) Aortic constricted and incompetent.

Aortic.	Mitral.	Pulm Artery.	Tricuspid.
·75 in.	1·3 in.	1·1 in.	1·7 in.

Here the result is essentially as in Class I., the effect upon the tricuspid being even less than in it.

(3) Aortic dilated and incompetent.

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
1·2 in.	1·7 in.	1·2 in.	2 in.

The result in this case is different from that in the two foregoing. As will be noticed, the effect of the dilated and incompetent aortic has been to *induce a general distension of all the other orifices.* It is to be explained simply by the wide incompetent aortic allowing of a sudden and full regurgitation of the arterial blood upon the left ventricle during diastole, that is to say, while the mitral valve is open. This diastolic

reflux continued for a sufficiently long time, by maintaining the pulmonary artery and the right chambers of the heart in a chronic state of distension, induces a widening of their orifices. The more constricted the aorta becomes, the less, naturally, will this direct regurgitant arterial pressure react upon the sound orifices.[1]

I do not find a single case in my records in which, when the aortic alone was diseased, it was constricted without being incompetent. The incompetency was, however, sometimes slight.

B. *Pure Mitral.*

(1) Mitral constricted and incompetent.

This constitutes by far the commonest deformity of the mitral resulting from old standing endocarditis. Old standing endocarditis causes thickening of all parts of the mitral. Not only does the substance proper of the valve suffer, but where the disease has been at all extensive the chordæ tendineæ will be found almost certainly to participate. This thickening diminishes the size of the intervals between the subdivisions of the chordæ, and ultimately fills these up so completely that the mass comes to resemble a solid fibrous pillar rather than an aggregation of isolated bands. At the same time the chordæ are dragged upwards towards the margin of the valve, and are so shortened that the tip of the musculi papillares and the edge of the valve may actually be in contact. The posterior wall of the ventricle is also pulled upon, and being thus bound to the mitral is retarded in its free action.

It accordingly follows that when the mitral is constricted, it almost to a certainty becomes incapable of accurately closing the orifice, and so allows of more or less regurgitation. The evil influence, however, of the defect upon the size of the other orifices is inappreciable, as the accompanying figures testify:—

Aortic	Mitral.	Pulm. Artery.	Tricuspid.
·97 in.	·86 in.	1·1 in.	1·7 in.

This result is probably to be explained by the constriction in a

[1] The mechanism of the arterial recoil is entered into more fully further on.

manner modifying the dilating tendency of the mitral regurgitance upon the orifices of the right side.

(2) Pure dilatation of the mitral.

A dilatation of the mitral with a competent and otherwise healthy aortic is a form of lesion only very seldom encountered. In the whole of my records of individuals dying from various diseases I can find but seven cases. A congenitally large mitral, with corresponding enlargement of all the other orifices, occurred in eleven cases. In only one case of mitral dilatation was there evidence of endocarditis, and in this single example it was of an acute nature and of septic origin. In none of the cases was it noted that a murmur was audible, although from the necessarily brief record of the history in the *post-mortem* journals, too much reliance should not be placed upon this statement.

Passing over, in the meantime, those which were evidently congenital enlargements, or at least in which the orifices were all equally dilated, let us examine the effect of the dilatation of the mitral upon the other orifices. The figures are the following:—

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
1 in.	1·68 in.	1·27 in.	1·98 in.

This practically shows that with a mitral of 1·7 in. diameter, the pulmonary artery and tricuspid corresponded respectively to close on 1·3 and to 2 in.

Most of the subjects unfortunately died from lung disease, and hence it is difficult to say in how far the dilatation of the right orifices was due to this cause. It should be mentioned, however, as supporting the belief that the dilated mitral was one of the chief factors in inducing the enlargement, that the dilatation of the right orifices was quite as great in those cases where the lungs were sound, or at any rate in which they were not the seat of disease unconnected with the cardiac condition.

C. *Aortic and Mitral combined.*

(1) Aortic and mitral both constricted; aortic competent, mitral incompetent.

It might have been expected that in this case the orifices on

the right side would have suffered dilatation. Such, however, as will be seen from the accompanying results, was not the case.

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
·7 in.	1 in.	1·1 in.	1·6 in.

It is probable that the constriction of the mitral, in these as under other circumstances, prevented the deleterious effects of the regurgitance through its orifice being felt.

(2) Aortic and mitral both constricted and both incompetent.

The measurements are the following:—

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
·8 in.	·77 in.	1·08 in.	1·6 in.

The only effect upon the orifices of the right side, be it a consequence or a mere coincidence, would appear to have been that of rendering them actually somewhat smaller than those of the average healthy heart, more especially as this class was taken entirely from males.

(3) Aortic of natural size but incompetent, mitral constricted and incompetent.

Nearly 50 per cent. of the cases were females, and, as will be seen, the effect upon the size of the orifices of the right side was inappreciable.

Aortic.	Mitral.	Pulm. Artery.	Tricuspid.
·97 in.	·87 in.	1·1 in.	1·6 in

D. *Tricuspid.*

The cases of tricuspid disease observed by myself were unfortunately all combined with disease of the left orifices, and hence no differential conclusions could be drawn from them.

Summary of the foregoing Results.

The data just enumerated bring out the somewhat remarkable result, that the only lesions of the valves of the left side which are accompanied by any appreciable distension of the otherwise sound orifices are *uncomplicated aortic regurgitance with a wide orifice*, and *uncomplicated dilatation of the mitral.* In the former of these, the other three orifices were

considerably above the average diameter, and in the latter, both the pulmonary artery and tricuspid were distended while the aortic remained of natural size. As regards the other classes, it may be noted that *where incompetence of a valve was accompanied by constriction of the orifice, the remaining apertures were not sensibly affected,* the legitimate conclusion deducible from this being that constriction of an incompetent orifice exerts a salutary influence in preventing distension of the other orifices of the organ.

On referring to the sequel it will be found that a constricted aortic and mitral lesion, where both are incompetent, occasions great hypertrophy of the right ventricle, whereas we have just seen it has but little influence upon the size of the right orifices. At first sight these results seem somewhat discordant, but may probably be explained in the following manner. The constricted aortic and mitral will prevent such a direct recoil of the arterial blood during diastole as would happen were they of natural size or dilated. This will tend to keep up a tonic state of high tension within the pulmonary circuit rather than to subject it to sudden exacerbations of pressure. Such a continuous strain in course of time might induce hypertrophy of the right ventricle, seeing that the ventricle will have to contract more energetically in order to open the pulmonary artery orifice, without the orifices becoming much enlarged. Where, however, the aortic and mitral openings are wide and where the aortic is incompetent, there must, in addition, be an instantaneous recoil of the arterial pressure upon the whole pulmonary system during each diastole, with a sudden tendency to stretch the right orifices, resulting most probably in a permanent distension of the latter and hypertrophy of the wall of the right ventricle.

Hypertrophy and Dilatation from Valvular Disease.

A. *Aortic.*

Although in the majority of aortic lesions hypertrophy of the left ventricle will be found to coexist, yet, as Gairdner[1] remarked, there is a capriciousness as to its presence or absence which is

[1] *Brit. and For. Med. Chir. Rev.*, vol. xxiii., 1853, p. 211.

sometimes difficult to explain. When the aortic is experimentally injured, its reserve energy, which, as shown by Rosenbach,[1] is considerable, is called forth. It contracts more vigorously, and does so until new muscular fibre is generated in sufficient amount to compensate for the defect. In course of time dilatation ensues,[2] and is followed by hypertrophy. Balfour states[3] that such is also the sequence of events in man.

Why does dilatation take place, and what is the increased work performed by the heart which calls forth the hypertrophy of its fibre?

Let us consider the simplest aortic lesion to begin with, namely,—

(1) Aortic incompetence without constriction or dilatation of the orifice, the mitral being normal.

The blood here, of course, will regurgitate from the aorta during ventricular disatole as a primary and immediate result, and the cavity will thus be filled from two sources instead of from one. Increased strain will be thrown upon the cardiac muscle from the arterial recoil, and there will be a much greater tendency to dilatation than in health.

The blood in a sound heart, at least during the first stage of diastole, flows passively into the ventricle, without receiving much if any impulse from the auricle. The latter contracts as it is becoming emptied and drives the remainder of the blood out of its cavity. The blood must therefore impinge against the ventricular wall with very little force during health, and hence the strain will be comparatively slight. It has even been said by Pettigrew[4] that the dilatation of the ventricle is a vital act.

In simple aortic regurgitation, however, the arterial recoil must be enormous, and it occurs during diastole. Rosenbach[5] found it to be sufficient to produce aneurism of the apex in animals in which the valve had been artificially destroyed.

The cause of the recoil is usually held to be the elasticity of

[1] *Arch. f. exp. Pathologie u. Pharmakologie*, vol. ix., 1878, p. 10.
[2] *Loc cit.*, p. 12.
[3] *Diseases of the Heart and Aorta*, 1876, p. 71.
[4] *Physiology of the Circulation*, 1874, p. 115.
[5] *Loc. cit.*, p. 14.

the arterial walls. It is, however, doubtless erroneous to regard this as the only cause. In estimating the factors which are instrumental in raising the blood-pressure, the arteries are commonly looked upon as if they were a series of exposed tubes. In reality, however, there is no part of the body in which the arteries or capillaries can be said to lie exposed. The nearest approach to it is in the case of the capillaries on the alveolar walls of the lung, but even here they are connected to an eminently elastic tissue and are covered by endothelium. In all other parts they are bound down by tissues more or less resilient (yellow elastic fibre, white fibrous tissue, muscle, &c.), whose interspaces are filled with liquid. This liquid will consequently tend to diffuse the elastic pressure of the tissues, and to bind it to that of the arterial wall.

Even in the abdomen the tissues are all so intimately and mutually applied to each other, that the abdominal contents may be regarded as a solid mass.

The skin and the immediately subjacent tissues are, finally, so elastic that they tend to complete a counterpoise sufficiently strong to resist the expansile efforts of the heart, transmitted throughout the whole body by the hydraulic machinery of the blood-vessels.

Donders[1] seems to have been the first to draw attention to this relationship of the arterial walls to the tissues encompassing them. He says, "We have previously seen that the blood-vessels do not bear the entire blood-pressure. They would become more expanded if they were not supported by the surrounding tissues. Part of the blood-pressure is expended upon the tissues and the nutritive liquids which bathe them."

Some years since I endeavoured[2] to demonstrate the importance of the influence exerted by this elastic reaction of the tissues in the processes of healing and organisation.

Landerer[3] has lately gone fully into the subject, and has

[1] *Physiologie d. Menschen.*

[2] *Journal of Anatomy and Physiology*, vol. xiii., 1879, p. 518; *Edinburgh Medical Journal*, vol. xxvii., 1881, p. 385.

[3] *Die Gewebsspannung in ihren Einflusse auf örtliche Blut und Lymphbeengung*, 1884.

estimated the power of recoil of the tissues in various parts and in different animals.

There cannot be much doubt that the subject of the relationship of the elasticity of the tissues, and of their contained liquids to the circulating blood, is one of the most profound in all pathology, and is one which has hitherto been much disregarded. We have been in the habit of attributing variations in the elasticity of the arteries exclusively to modifications of the arterial wall. It must, however, be sufficiently ostensible on reflection, that, as the arterial and capillary coats and the surrounding tissues and liquids may practically be regarded as continuous, and as constituting one texture, any modification in the elasticity of the fibre of the latter, or any difference in the quantity of liquid lying in the interspaces of the tissue, must react upon the blood in the vessels in very much the same manner as the arterial wall itself.

During muscular exertion, moreover, the pressure of these liquids will be increased, and will constitute at least one of the factors which go to raise the pressure in the arteries generally and in the aorta.

In aortic regurgitance all such exacerbations of pressure have to be borne by the ventricular wall, the mitral orifice, the lung, and the right side of the heart; and the larger the aperture of the aorta, as previously pointed out, the more suddenly will the returning gush of blood impinge upon them, and the greater will its influence for evil consequently prove. The mitral orifice and those orifices on the right side, as already demonstrated, will accordingly become unnaturally large, and the cavities of the ventricles will also increase in capacity.

The dilatation of the ventricle would, no doubt, continue to be progressive were means not forthcoming to withstand the undue backward strain brought to bear upon its interior. This is to be sought *in the hypertrophy of the muscular fibre.* The mass of new muscle maintains the tone of the heart, as that of the hypertrophied arteries maintains the arterial tone in cirrhotic Bright's disease or other chronic affection accompanied by a high arterial pressure.

The muscle of the heart, like involuntary muscle surrounding other cavities, has a *twofold* action. *It drives out the*

contents of the cavity, and it prevents over-distension. It is thus engaged, not only in propelling the blood, but also in maintaining the tone of the heart-wall. It is otherwise difficult to explain how the heart, even in health, with the constant filling of its cavities, does not in time become distended. The heart-muscle, in health, seems to possess a tonic function analogous to that of the musculature of the arteries, and this is brought more especially into play when the aortic blood is allowed, through insufficiency of the valve, to recoil upon the interior of the ventricle during diastole.

This tonic function of the heart-muscle is often overlooked, but must be one of very considerable importance.

Gaskell,[1] in summing up the results of his admirable paper on the innervation of the heart, concludes that muscular tissues exhibit three modes of responding to stimulation. Certain muscles possess essentially the power of "tonic contraction," others the power of "rhythmical contraction," and others that of "rapid contraction."

The striated muscle of vertebrates is characterised by—

> *Rapidity of contraction being most highly developed,*
> *Tonicity rudimentary,* and
> *Rhythmic action still more rudimentary.*

Cardiac muscle by—

> *Rhythmic action being most highly developed,*
> *Rapidity of contraction well marked,* and
> *Tonicity well marked.*

Unstriped muscle by—

> *Tonicity being most highly developed,*
> *Rhythmic action well marked,* and
> *Rapidity of contraction most rudimentary.*

It is indeed probable that the muscular fibre which surrounds any hollow viscus in the body subserves the purpose of maintaining the tone of the organ, and of thus preventing over-distension of its cavity. The muscular fibre of the arteries hypertrophies when unduly great distensile strain is put upon their walls, so does that of the bronchi and bladder, and it is only reasonable to suppose that the heart-muscle hypertrophies under like circumstances.

[1] *Journal of Physiology,* vol. iv. pp. 116–118.

The recoil of the arterial blood upon the interior of the ventricle will then be one of the main obstacles which the heart, in this disease, will have to overcome, and this will constitute in the case we are supposing, the chief, if not the only increased work to be done.

The ventricle meets the increased strain thrown upon it while it is filling, probably by being thrown into a series of small contractions before the true systole commences, and hence, possibly, the cause of the jar sometimes communicated to the finger in aortic regurgitant disease.

Marey[1] gives a curious tracing from the carotid artery of a person who suffered from aortic insufficiency, in which numbers of small secondary waves are seen in the diastolic part of the tracing and during the period of rest preceding the ventricular contraction. He interprets these as being caused by irregular contraction of the auricle. The phenomenon, however, might be explained by the aortic blood suddenly injected upon the wall of the ventricle throwing the latter into a series of spasmodic contractions of minor import previous to the occurrence of the true ventricular systole.

Such being one of the sources of overwork to be performed by the heart in the lesion we are at present contemplating, let us next consider what further overwork it has to undertake.

In health the pressure of the blood in the ventricle has to rise superior to that of the blood in the aorta before the aortic valve will open. If the valve is destroyed, and if the orifice be of natural calibre, will the intraventricular pressure have to reach a higher pitch before the blood will leave it to pass into the aorta? Obviously not, for the arterial pressure, there is good reason to believe, remains the same as before. The function of the valve is only called into play during the diastole of the ventricle; it is in abeyance, and might as well be absent during systole.

Rosenbach[2] found that in dogs and rabbits extensive destruction of the aortic, mitral, or tricuspid had no material effect in altering the arterial blood-pressure. In rabbits which were

[1] *La Circulation du Sang a l'état physiologique et dans les maladies*, 1881. p. 679.

[2] *Arch. f. exp. Pathologie u. Pharmakologie*, vol. ix., 1878, p. 1.

allowed to live for different periods after the valves were rendered incompetent, the arterial pressure was still uninfluenced. If, moreover, the orifice of the aorta were narrowed by the introduction of a sound, still no effect followed.

De Jager[1] obtained the same results in dogs after insufficiency of the aortic, mitral, or tricuspid had been artificially established, but in rabbits an absolute fall in the arterial pressure was noticed.

Under any circumstances, therefore, the ventricle will probably not be subjected to overwork in uncomplicated regurgitant aortic from having to overcome increased arterial pressure. It might possibly act at a disadvantage during systole were the cavity dilated, and where, consequently, a greater mass of blood would have to be propelled forwards than in health, but were the cavity not increased in size, the overwork thrown upon its wall would chiefly be that of resisting arterial recoil during diastole and of so maintaining the tone of the organ.

Conclusion.—*The overwork performed by the heart, in aortic regurgitance with a normal sized orifice, is chiefly that of keeping up the ventricular tone. If dilatation of the ventricle coexist, increased propulsive efforts may be required.*

(2) Aortic incompetence with a dilated orifice, mitral normal.

Here the conditions are simply an exaggeration of those in the preceding. From the fact that the wide orifice will permit of a less impeded arterial recoil, the impulse communicated to the interior of the ventricle by the sudden reflux of blood will be more sudden than in the former, and hence the strain during the commencement of diastole will be greater. There will, however, be if anything less difficulty in propelling the blood through the widened orifice during systole than before, and hence the increase of *propelling power* of the ventricle will be called for only where the cavity is much dilated.

As a matter of fact, I find from my average statistics that the cavities of the ventricles in this class of cases are not so large as in that immediately preceding (3¾ inches for each side, as compared with 4 inches for the left, and 4½ inches for the right), but that the ventricular wall is thicker. It may possibly be that

[1] Virchow and Hirsch's *Jahresbericht*, 1883, ii. p. 142.

the wide aortic orifice throws so great a strain upon the ventricle that the muscle hypertrophies before dilatation has reached so high a pitch.

Conclusion.—*The chief overwork performed by the heart, in aortic regurgitation with a wide orifice, is in keeping up the tone of the ventricle.*

(3) Aortic regurgitance with a constricted orifice, mitral normal.

The effect of constriction, in addition to the incompetence, will be two-fold. It will lessen the arterial recoil, or, at any rate, will permit of the blood regurgitating less suddenly than where the orifice is wide, and at the same time it will tend by narrowing the outlet to render the difficulty of propelling the blood forwards during systole greater.

The shock communicated to the interior of the ventricle will, accordingly, be less than where the orifice is wide, and hence, probably, the hypertrophy ought not to be so great as in either of the two preceding forms of disease. As will be seen from the following tabulated account of the effects of aortic disease on the wall, this is borne out in fact. The constriction of the orifice will thus in a manner compensate for the regurgitation and diminish the hypertrophy or dilatation which would otherwise follow. The constriction, on the other hand, will hinder the blood from passing out of the ventricle, and will therefore reflect its influence upon the wall. If the ventricle empties itself, it is clear that pure aortic constriction never could cause a dilatation. If a distended hollow viscus be compressed on all sides from without inwards, it will never become dilated. It is during diastole that dilatation alone can be effected, the pressure then being from within outwards, instead of from without inwards as in systole.

Of course it might be urged that the ventricle empties itself incompletely at each systole, and therefore the blood tends to accumulate within it. This is, however, matter of pure theory, and may well be called in question. If blood tends to accumulate in a chamber of the heart—where does the accumulation end?

I would therefore trace the cause of the hypertrophy in this lesion, firstly, to regurgitation of the arterial blood during

diastole, and, secondly, to the increased efforts required to be put forth by the heart-wall during systole. The effect of the regurgitance, however, will be modified by the constriction, and hence will be less injurious than where the orifice is of full size or dilated. The sum of the effects of both agents might come to be very much the same in regard to the condition of the wall as the single effect of a dilated incompetent orifice or one of natural size.

Conclusion.—*The overwork performed by the heart, where the aortic is incompetent and constricted, is two-fold, namely,* (1) *that of keeping up the tone of the ventricle, and* (2) *that of driving the blood through a narrow orifice.*

Comparative Effects of the foregoing Three Forms of Aortic Disease upon the Ventricular Walls and Cavities.

The above three forms of disease of the aortic constitute by far the largest proportion of pure aortic cases. As previously mentioned, I have failed to find in my records a single instance of a simple constricted aortic without the valve being, after death, incompetent, although sometimes only slightly so. The following statement gives a tabular view of the influence exerted by the three forms of aortic disease referred to upon the walls and cavities of the ventricles:—

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
1. Aortic normal diameter and incompetent.	4 in.	$4\frac{1}{2}$ in.	$\frac{5}{8}$ in.	$+\frac{3}{16}$ in.
2. Aortic constricted and incompetent.	$3\frac{1}{2}$,,	$3\frac{1}{2}$,,	$\frac{5}{8}$,,	$+\frac{1}{8}$,,
3. Aortic dilated and incompetent.	$3\frac{3}{4}$,,	$3\frac{3}{4}$,,	$+\frac{3}{4}$,,	$+\frac{1}{4}$,,

It would thus appear that where the orifice was of natural size the left ventricle was largest, that it was of medium capacity where the orifice was dilated, and that it was smallest where the orifice was constricted. The explanation of these facts has already been sufficiently entered into.

It will, however, be noticed that the thickness of the wall was

greatest where the orifice was largest, least where it was of natural size or constricted; and this is exactly what should be expected. The greatest arterial recoil takes place with the dilated aortic, the least with the constricted. In the case of the constricted, however, the impediment to the propulsion of the blood constitutes an additional cause of hypertrophy, and hence there is good reason for the wall being as thick as the figures show it to be.

We have previously seen that the dilated regurgitant aortic also exerts the most injurious distensile effect upon the other orifices, and, consequently, there is little doubt that this form of valvular disease is one of the most disastrous to which a heart can be subjected. The more suddenly the defect is brought about, the greater the danger. It is accompanied in larger proportion than any other cardiac lesion by the evils which follow in the train of free regurgitant arterial pressure.

Coexistent Dilatation of Right Ventricle.—It was a good many years ago remarked by Gairdner[1] "that he had never seen an instance of hypertrophy affecting *the left side alone.*" Contrary to what less accurate observers frequently affirm, there is an immense deal of truth in this statement, not only as relating to hypertrophy, but also as bearing upon the size of the cavities.

From the foregoing statistics of aortic disease, it will be noticed that the size of the right ventricle had advanced almost *pari passu* with that of the left, and, indeed, in one class of cases had overreached it. There was also a certain correspondence in the thickness of the wall of the right ventricle as compared with that of the left, probably accounted for by the regurgitant pressure indirectly influencing the whole right side of the circulation.

Cause of Hypertrophy of Musculi Papillares.—This depends upon their functions being overtaxed like that of other parts of the heart-wall. It is most likely that the musculi act as a stay upon the valve to which they are attached, and thus prevent eversion during systole. Pettigrew[2] describes the cusps of the mitral as being floated up during the ventricular diastole. During systole, however, the blood is thrown by the action of the

[1] *Brit. and Foreign Med. Chir. Rev.*, vol. xxiii., 1853, p. 218.
[2] *Physiology of the Circulation*, 1874, pp. 278–280.

ventricle into spiral columns and twists them into each other, while the musculi papillares drag them downwards.

M. Sée[1] says that the papillary muscles contract at the same time as the ventricles. They tighten the chordæ and pull the cusps down. The left cusp of the mitral plays much the more active part in closure, but the right is not unemployed. The musculi might accordingly be expected to hypertrophy where the aortic orifice is constricted, for here the increased effort required to propel the blood through the narrow aortic orifice will react upon the mitral cusps and tend to force them upwards.

Effect of Filling of the Left Ventricle from Two Sources.—As the left ventricle is filled both from the aorta and from the auricle in aortic regurgitation, it follows that there must be a mixing of the blood from the two sources of supply within the chamber. The gross effect will of course be that the amount of blood passing directly from the lungs into the aorta will be less than in health.

The proportion in which the auricular and aortic bloods mix constitutes an interesting and as yet undetermined question. The pressure within the pulmonary artery, as compared with that of the aorta, has been variously estimated as something like 2 : 5 or as 1 : 3. The pressure within the pulmonary veins is considerably less, while within the auricle, at least towards the end of the auricular systole, it is again somewhat increased, but still considerably below that of the blood within the aorta. More blood should therefore regurgitate from the aorta than would pass into the ventricle through the auriculo-ventricular opening. The auriculo-ventricular opening, however, is larger than the aortic, and hence there should be less obstacle to the free passage of the auricular blood than to the regurgitation of the systemic.

The pulmonary veins are without valves, and the regurgitation from the aorta occurs during diastole, and hence at a time when the auriculo-ventricular orifice is open. It might *a priori* be expected that if the pressure within the aorta be greater than that in the auricle, injurious influences would be brought to bear directly upon the lung. Such is often the case, but not

[1] *Archives de Physiologie*, vol. i., 1874, p. 552.

always. It is a well-known fact that individuals with aortic disease are frequently unconscious of it until they undergo a medical examination for life insurance or for some other reason. The heart evidently accommodates itself to the altered circumstances, a result which might be accounted for by the pulmonary veins rhythmically closing as the auricle begins to contract. If some provision of this kind were not forthcoming, it is difficult to see how the circulation could continue unimpeded for any length of time.

If the orifices of the pulmonary veins do close, and if the hypertrophied ventricle keeps up the heart's tone, then it is possible to conceive that, with each systole, blood is propelled forwards composed say of two parts aortic and one part auricular. This might naturally be held to occasion such an under-oxygenation of the blood as to materially deteriorate its respiratory qualities, and in certain cases it is so. It must be remembered, however, that if the blood is delayed in its passage through the lung, and if the bronchi and air-vesicles are unobstructed, it becomes hyperoxygenated. Hence, although the fresh blood from the lung circulates less freely, yet its hæmoglobin may be of such a high respiratory capacity as in a manner to compensate for the defect. If, moreover, the auricle were to hypertrophy, the blood would be driven into the dilating ventricle with impetus sufficient to, in a manner, equal or exceed that caused by the arterial recoil.

Landois[1] remarks that hypertrophy of the left auricle occurs as a result of aortic insufficiency, "because the auricle has to overcome the continual aortic pressure within the ventricle." As a matter of fact, however, it will be found that hypertrophy of the wall of the left auricle in this disease is not of common occurrence, but that the cavity, as a rule, is slightly dilated. The dilatation is not so extensive, however, as when the aortic regurgitance is complicated with mitral incompetence and stenosis, for under these circumstances the forces tending to dilate the auricle are of a threefold nature. In the first place, there is the arterial recoil during ventricular diastole; in the second, the hindrance to the free passage of blood from

[1] *Text-book of Human Physiology*, English translation by Stirling, 1885, vol. i. p. 80.

the auricle into the ventricle owing to the constriction of the auriculo-ventricular orifice, also occurring during diastole; and, in the third, the regurgitant systolic impetus conveyed to the auricle during systole. The auricle in this form of disease will be found to be larger than in any other, while in pure mitral disease it is usually of medium capacity.

Hypertrophy does not follow lesions of the orifices with the same facility in the case of the auricles as in that of the ventricles. Hence the abnormal conditions of pressure arising from valvular disease will be found more often to leave their record in auricular dilatation, rather than in an increased thickness of the walls.

B. *Mitral.*

(1) Mitral incompetence with stenosis, aortic normal.

In this, which is the usual form of mitral disease, it might theoretically be expected that the tendency to hypertrophy and dilatation of the left ventricle would be less than in aortic incompetence. There is no arterial rebound upon the ventricular wall during diastole, and from the narrowing of the mitral orifice the blood will be impeded in its flow from the auricle, and hence might not reach the ventricle even with such force as is imparted to it in health.

There is, however, a cause for hypertrophy in this class of cases which is absent in simple aortic disease. The incompetent mitral allows part of the ventricular blood to recoil during systole upon the left auricle, and this will naturally tend to weaken the impulse communicated to the systemic vessels. The ventricle will thus have to work harder in order to keep up the arterial pressure.

Artificial destruction of the mitral in an otherwise healthy animal does not cause a fall in blood-pressure. This is probably to be explained by the ventricle contracting more vigorously, and by the openings of the pulmonary veins closing sufficiently to limit the regurgitant effects to the auricle.

It is very unlikely, however, that the orifices of these vessels would withstand the dilating influence of this regurgitance for long. There is every probability that if the thin wall of the auricle became stretched they would widen, and thus allow of

the influence of the ventricular systole being felt by the whole pulmonary circulation as far back as the pulmonary artery orifice.

The result ought to be, as the following figures show is the case, that this lesion of the mitral induces slight hypertrophy of the wall of the left ventricle.

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
Mitral constricted and incompetent.	+ $3\frac{1}{4}$ in.	+ $3\frac{1}{2}$ in.	$\frac{3}{8}$ in.	$\frac{1}{8}$ in.

Rosenstein[1] remarks that in this valvular defect the left ventricle is so small, as compared with the dilated right, that it looks almost like an appendage of the latter. The above figures do not entirely support this statement. The difference in the dilatation of the two cavities, as will be noticed, was comparatively slight, and there was no appreciable hypertrophy of the right.

(2) Mitral dilated, aortic normal.

This being a rare condition, and not always accompanied by regurgitation, it is difficult to say what its actual effects might be. The large mitral, of course, if incompetent, would allow a still greater reflux than in the foregoing. The combination of a dilated mitral orifice with any amount of incompetency must, however, be looked upon somewhat in the light of a pathological curiosity.

The following figures may be taken for what they are worth:—

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
Mitral dilated, but doubtful whether incompetent.	$8\frac{3}{4}$ in.	4 in.	+ $\frac{1}{2}$ in.	$\frac{3}{16}$ in.

[1] *Cyclopædia of Practice of Medicine*, edited by von Ziemssen, English translation, vol. vi. p. 126.

(3) Mitral constricted but competent, aortic normal.

This, as previously indicated, is also a rare lesion. The commonest cause of it is the projection into the funnel-shaped valve of vegetation or calcareous masses, tumours, &c. In other instances the margin of the valve is alone contracted without the entire valve being converted into a leather-like structure, a condition which apparently is compatible with the valve closing.

The effects of such a lesion would, of course, be to hinder the blood in its transit from the auricle to the ventricle, unless the auricle compensatorily hypertrophied to drive it onwards with increased force.

C. *Aortic and Mitral combined.*

(1) Aortic and mitral both constricted and both incompetent.

Here the left side of the heart may be regarded as devoid of valves, and with its orifices so constricted that the blood is trammelled in its passage through them. It is a rhythmically-contracting tube unprovided with competent valves at either end. The systemic arteries thus become directly continuous with the pulmonary; they form one set of vessels with this rhythmically-contracting chamber—the mutilated auricle and ventricle—between them. The scheme of the circulation in fact comes to resemble that of the fish. There is in reality one auricle and one ventricle (the right); with a vessel (pulmonary artery) conducting to the lungs; vessels conveying the blood (pulmonary veins) to a pulsatile vessel or chamber (the left auricle and ventricle), thence to the systemic arteries. The ultimate result must be, of course, that during ventricular diastole the pressure within the pulmonary vessels as far back as the nearest obstruction, *i.e.*, the pulmonary artery orifice, will tend to be equalised with that in the systemic arteries. In fact, if the mitral fails to close, and if its aperture, although narrow, remains larger than the constricted aortic, as usually happens, the ventricular blood ought by preference to pass backwards through the mitral instead of forwards into the aorta. The lung would thus have imparted to its vessels actually more of the ventricular energy than is exercised upon the systemic arteries, the only counter-

balancing agent being the pulmonary blood which is being driven in the opposite direction by the right ventricle.

The pulmonary capillaries would thus have to bear at each ventricular systole both the pressure imparted to them by the right ventricle and the regurgitant pressure from the left. They are not even free from injurious over-pressure during ventricular diastole, because they are then subject to the backward recoil of the whole arterial system.

It cannot be a matter of wonder that under these circumstances the delicate-walled capillaries of the lung, entirely unsupported as they are on one side, should become converted into huge nævus-like masses. They in fact have to support from three to five times the pressure they were originally intended to bear, and it is only because they are so distensile that the effects of this do not prove to be more disastrous than they are.

But where does this regurgitant effect cease? Theoretically, it ought not to be felt beyond the next lock, that is to say, beyond the orifice of the pulmonary artery, provided that the valve of this vessel remains competent. The orifice is very rarely altered in size, and the incompetency of the cusps is a thing almost unknown. The sharpness with which they can be heard to click together in valvular disease of the left side is evidence of their timely and often premature closure.

How do the organs on the right side of the heart therefore come to suffer?

We have seen that in the majority of valvular lesions of the left side the tricuspid and pulmonary artery orifices are not altered in diameter. It might, therefore, well be argued that so long as the pulmonary artery orifice is competent, the regurgitant pressure imparted to the lung could not possibly affect the organs further back. Yet pulsation may be felt and seen in the jugulars and in the liver in such cases with every ventricular systole.

The right ventricle will undoubtedly have more to do in such a case than in health, because before the sigmoid segments will relax, the pressure of the blood within the right ventricle will have to rise superior to that in the pulmonary artery. Its muscular fibre will therefore tend to hypertrophy, as the accompanying figures demonstrate:—

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
Aortic and mitral both constricted and both incompetent.	3½ in.	3½ in.	+½ in.	+¼ in.

When this hypertrophied muscular fibre contracts the blood will press injuriously against the tricuspid valve. This valve at no time is perfectly competent in man, and when increased strain is thus put upon it, it will become much less so than it is naturally. Hence blood will regurgitate and cause the pulsation and other injurious effects so common in such cases. The amount of evil occasioned would thus be proportionate to the extent of the hypertrophy of the right ventricle, and the great diversity noticed in the state of the liver, kidney, and other organs in various forms of valvular heart affection may thus be accounted for. In some instances there is mere congestion of these organs, in others not even this, while in yet others they have suffered extreme atrophy.

An *emphysematous lung* may cause hypertrophy of the right ventricle, and in this case also the same effects are noticed in distant organs. The injury in both cases is inflicted during the systole of the right ventricle. It is while the walls of this chamber are contracting, not while they are in a state of relaxation, that the destructive backward impulse, rendering their valves incompetent, is conveyed to the large veins.

If the ventricle failed to empty itself, and if distension of its cavity was thereby occasioned, the tendency to render the tricuspid incompetent would be increased. We do not know, however, whether this takes place. It must, moreover, be remembered that simple distension of the right ventricle would probably never induce a tricuspid regurgitation, if the pressure within the pulmonary vessels remained normal, because the blood even from a distended ventricle would by preference run through the pulmonary artery rather than backwards through the tricuspid. Where the pressure within the pulmonary artery is above that of health the ventricle must contract more

energetically to lift the pulmonary artery lock, and even after this has been accomplished the blood will continue to be opposed by this over-pressure during the whole time the valve is open; hence the overwork performed by the ventricle will have to be sustained. It is only reasonable to believe that this, in course of time, must react injuriously upon the tricus pid andadd to its natural incompetence.

Conclusions.—*The increased work performed by the left chambers of the heart in this form of disease is in keeping up the arterial pressure. Part of the energy so liberated is expended upon the pulmonary circulation, which, by raising the pressure within the pulmonary vessels, necessitates increased effort on the part of the right ventricle in opening the pulmonary artery valve. This is frequently followed by hypertrophy of the ventricular walls. The unusually energetic contraction also reacts upon the naturally incompetent tricuspid and renders it more incompetent, thus affecting deleteriously the whole venous circulation.*

(2) Aortic of natural size but incompetent, mitral constricted and incompetent.

The conditions here, so far as the effects on the right side of the heart are concerned, are probably more favourable than in the former case. As the aortic is of normal size the blood will pass more easily through its orifice, and hence will not tend to regurgitate so freely through the incompetent mitral. The amount of hypertrophy of the right ventricle ought for this reason to be less than in the foregoing example, because the blood of the right ventricle will experience less opposition in being propelled into the pulmonary artery. The following are the actual average measurements:—

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
Aortic of natural size but incompetent, mitral constricted and incompetent.	$3\frac{1}{2}$ in.	$+3\frac{1}{2}$ in.	$\frac{1}{2}$ in.	$+\frac{1}{8}$ in.

It might be argued that the wider aortic orifice will allow more blood to regurgitate during diastole; but it is questionable whether this, seeing that the mitral is constricted, would be so injurious in the long run as the regurgitance of the ventricular blood during systole, where in addition to the mitral constriction the aortic is also of narrow calibre.

(3) Aortic and mitral both constricted, aortic competent, mitral incompetent.

The argument based on the figures under the class just considered (No. 2) gains strength from those accompanying this.

	Ventricles.		Walls (Maximum thickness).	
	Left.	Right.	Left.	Right.
Aortic and mitral both constricted, aortic competent, mitral incompetent.	$3\frac{1}{8}$ in.	$3\frac{1}{4}$ in.	$\frac{1}{2}$ in.	+ $\frac{1}{8}$ in.

In this case one element of regurgitant pressure is removed as compared with Class 2, namely, the aortic incompetency. There is superadded another, however, the aortic constriction. The figures remain very much as before, showing that *with an incompetent mitral*, aortic constriction has much the same effect upon the thickness of the walls and size of the cavities as aortic regurgitance. Where incompetency of the aortic is combined with constriction of its orifice, however, as in Class 1, the difference in the effects is demonstrated by the greater thickness of the walls, both of the left and of the right ventricles.

D. *Tricuspid Stenosis.*

The cases of this lesion that have come under my personal notice, as before mentioned, have been so complicated with disease of the orifices on the left side, that it is impossible to form from them an accurate idea of what the result on the walls and cavities of the heart would be.

Concluding Remarks on Hypertrophy from Valvular Disease.

It must be remembered that the heart when deprived of its natural locks may still have a certain inherent power of driving the blood onwards. Just as the œsophagus seizes the draught of liquid, and conducts it to the stomach even against gravity, so the heart may be supposed to do the same with the blood.

Pettigrew has described the ventricle as twisting the mass of blood within it in a spiral manner. If the heart-wall has no further hold upon the blood than a mere contractile sac, it is hard to conceive, where perhaps three of the valves are diseased, how the circulation continues to maintain even the desultory course that we know it does.

It should also be borne in mind that an impaired valve need not be a totally useless valve. It may subserve its purpose in an incomplete manner.

The chief redeeming point in valvular disease of the heart probably is that the pulmonary semilunes are seldom incompetent. This in a manner separates the venous from the arterial circulation, and prevents the pressure on both sides from becoming equalised.

Connected Tabular Statement of the Measurements referred to in the Foregoing Paper, along with the Average Weights (Males and Females included).

	Weight in ozs. Avoird.	Orifices.				Cavities.		Walls (Maximum thickness).	
		Aortic.	Mitral.	P. Art.	Tricusp.	L. Ven.	R. Vent.	L. Vent.	R. Vent.
1. Normal heart.	10–13 oz.	0·9–1 in.	1·2–1·4 in.	1·1–1·2 in.	1·5–1·8 in.	3–$3\frac{1}{4}$ in.	$3\frac{1}{16}$–$3\frac{3}{8}$ in.	$\frac{1}{2}$ in.	$\frac{1}{8}$ in.
2. Aortic of normal size but incompetent.	$21\frac{3}{4}$ "	0·99 "	1·3 "	1·1 "	1·8 "	4 "	$4\frac{1}{2}$ "	$\frac{5}{8}$ "	$+\frac{3}{16}$ "
3. Aortic constricted and incompetent.	$18\frac{3}{4}$ "	0·75 "	1·3 "	1·1 "	1·7 "	$3\frac{1}{2}$ "	$3\frac{1}{2}$ "	$\frac{5}{8}$ "	$+\frac{1}{8}$ "
4. Aortic dilated and incompetent.	$22\frac{3}{4}$ "	1·2 "	1·7 "	1·2 "	2 "	$3\frac{3}{4}$ "	$3\frac{3}{4}$ "	$+\frac{3}{4}$ "	$+\frac{1}{4}$ "
5. Mitral constricted and incompetent.	16 "	0·97 "	0·86 "	1·1 "	1·7 "	$+3\frac{1}{4}$ "	$+3\frac{1}{2}$ "	$\frac{5}{8}$ "	$\frac{1}{8}$ "
6. Pure dilatation of mitral.	$20\frac{1}{2}$ "	1 "	1·68 "	1·27 "	1·98 "	$3\frac{3}{4}$ "	4 "	$+\frac{1}{8}$ "	$\frac{3}{16}$ "
7. Aortic and mitral both constricted, aortic competent, mitral incompetent.	$12\frac{3}{4}$ "	0·7 "	1 "	1·1 "	1·6 "	$3\frac{1}{8}$ "	$3\frac{1}{4}$ "	$\frac{1}{2}$ "	$+\frac{1}{8}$ "
8. Aortic and mitral both constricted and both incompetent.	$20\frac{1}{4}$ "	0·8 "	0·77 "	1·08 "	1·6 "	$3\frac{1}{2}$ "	$3\frac{1}{2}$ "	$+\frac{1}{2}$ "	$+\frac{1}{4}$ "
9. Aortic of natural size but incompetent, mitral constricted and incompetent.	$20\frac{1}{2}$ "	0·97 "	0·87 "	1·1 "	1·6 "	$3\frac{1}{2}$ "	$+3\frac{1}{2}$ "	$\frac{1}{2}$ "	$+\frac{1}{8}$ "

ON A NEW ACID FOUND IN HUMAN URINE WHICH DARKENS WITH ALKALIES (*ALCAPTONURIA*).

By ROBERT KIRK, M.D. Edin., F.F.P.S. Glasg.

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THE further investigation of this subject, on which a former paper appeared in the *British Medical Journal* of November 17, 1886, has opened up a wider field of inquiry than was at first anticipated, and has led to novel and interesting results.

Among previous researches on alcaptonuria may be mentioned those of Bödeker,[1] of Ebstein and Müller,[2] and of Professor Smith[3] of Dublin. The first of these isolated a substance from the urine to which he gave the name of alcapton, and which contained nitrogen, although the presence of this element was no doubt due to impurity. Ebstein and Müller, on the other hand, found, as they supposed, pyrocatechin in the urine, and Professor Smith protocatechuic acid. In the article above referred to, I pointed out that by concentrating the urine to an eighth or a tenth, either slowly over the water-bath or by boiling, subsequently acidulating with hydrochloric acid and extracting with ether, a new body was obtained, to which I gave the name of *urrhodinic acid*, which differed widely from any of the compounds above mentioned, and the properties of which accounted for all the peculiar reactions of the urine. This method, indeed, is actually given by Méhu[4] as a means of extracting pyrocatechin from the urine, but none of those who have examined cases of alcaptonuria seem to have followed it. It may be mentioned, however, that Fleischer,[5] in his

[1] *Annal. der Chem. und Pharm.*, Bd. cxvii. 98, 1861.

[2] Virchow's *Archiv*, Bd. lxii. S. 554, 1875.

[3] *Dublin Med. Jour.*, vol. ii. p. 465, 1882.

[4] *L'Urine Norm. et Patholog.*, p. 117. Here speaking of salicylic acid, he refers to the use of a mineral acid (sulphuric) as applicable to the extraction of oxyphenic acid (pyrocatechin) and other acids from the urine, although, in treating specially of pyrocatechin further on, he does not again mention this.

[5] *Berliner Klin. Wochenschrift.*, Sept. 1875, Nos. 39 and 40.

investigations of the urine of patients taking large doses of salicylic acid, and in which he is said to have found pyrocatechin, adopted this plan of isolating it, which he calls Bertagnini's method. But it is quite clear from his descriptions that none of the urines examined by him at all resembled that of alcaptonuria, or contained any of the remarkable substance which I have called urrhodinic acid; otherwise, he could not have failed to find it. The mass of crystals obtained by this process from the urine of alcaptonuria is, in my experience, quite unique, both in quantity and character, and, besides the urine of the horse and cow, I have examined that of patients taking large quantities of salicylic and carbolic acids. Some of the urrhodinic acid exists free in the urine, an equal volume of ether taking up about one-twentieth of the entire amount it contains. After acidulation with hydrochloric acid, however, the ether at once abstracts one-half of the peculiar substance which gives the colour with alkalies. It must be evident that we thus obtain the object of which we are in quest, whether in a pure state or not.

In further prosecuting this inquiry, I have often had, as before, the co-operation of the Rev. Mr Gibson, who has devoted much time to chemical pursuits, and who is extremely careful and accurate in his methods of investigation. Our former conclusion has been fully confirmed, but the urine has been found to yield not one, but two new acids. Some facts mentioned in my former paper, and others afterwards observed, soon made it appear that what we have called urrhodinic acid was not a true chemical compound, but a mixture of two or more substances. By keeping specimens of it exposed to heat, air, and moisture for certain periods of time, and by varying the preparation of it in various ways, it was found that its properties were not uniform. It was noticed, for instance, that some samples gave a much redder watery solution than others, and that these had less marked reducing actions and gave less colour with alkalies, besides containing sometimes a considerable quantity of a dark humus-like powder, insoluble in water. It appeared not only that there were several constituents in the mixture, but that some of these might be increased at the expense of others, thus proving a certain relationship to exist between them. We were

long at a loss to understand what was taking place, and were baffled in our attempts to separate these bodies from each other. At length a more careful examination of the action of neutral lead acetate fortunately enabled us to effect the latter object. As previously stated, urrhodinic acid gives white precipitates with both neutral and basic lead acetate. It was found, however, that the neutral salt did not throw down the whole of the ingredients, but left a pale yellow filtrate which possessed the aromatic odour of the original substance, and which darkened with alkalies and exercised reducing actions as before. Further, the precipitate, if allowed to form gradually, was not white, but consisted of two distinct portions, a pale and a dark, the latter being most abundant in the redder solutions of the mixture. The dark precipitate always fell first, while the pale one formed more slowly, even in concentrated solutions; and the two differed from each other in various physical properties. It became necessary to obtain these several bodies in an isolated form, and various methods of separating them were tried. A good deal of trouble was here experienced, and many specimens were spoiled from various causes, especially during evaporation *in vacuo* over sulphuric acid, for which our apparatus, depending on a variable water pressure, was at first defective, while other samples were found at the end of the process to be too small in quantity to admit of an organic analysis and a thorough examination of the substance. We will limit the present paper chiefly to an account of the body obtained from the pale precipitate, as this has been perfectly isolated and analysed and is not only different from anything previously supposed to exist in the urine of alcaptonuria, but also, so far as known to us, new to chemistry. It assumes a definite crystalline form, and among its interesting properties must be specially mentioned its power of throwing down the black suboxide of bismuth when boiled with an alkaline solution of the nitrate, this being a new fact in alcaptonuria; while it appears to be the source whence the other bodies are derived, whether in the animal system or in the process of analysis. After various trials it was found best to prepare it as follows.

A concentrated solution of the mixed substances is prepared by dissolving them in a small quantity of hot, but not boiling,

water, and this is filtered to remove any trace of the insoluble powder already mentioned. To the filtrate, which has a deep red colour, a saturated solution of lead acetate is now gradually added, and the dark precipitate which falls removed by repeated filtration. It is well to use several filters simultaneously for this purpose when it is desired to preserve this precipitate also, for it is so viscid that it is extremely difficult to detach it from the filter after a certain length of time. If this fractional precipitation is cautiously conducted, a specimen is at length obtained which consists of a mixture of the dark and light precipitates. The filtrate is now of a yellow colour with a tinge of brown, and any further precipitate obtainable is of a pale colour. To avoid further dilution the liquid is now transferred to a mortar, and some solid lead acetate is pounded amongst it with the pestle. In a few seconds a cream-coloured precipitate forms, consisting of the lead salt of the object of our search and some excess of lead acetate. The filtrate from this has a pale yellow colour, but all the aromatic odour of the original solution, and gives no further precipitate with neutral lead acetate, but a white precipitate with the basic lead salt.

The above precipitate is now washed on the filter with water until the washings cease to have an acid reaction. As it forms readily only in strong solutions, so it is partly soluble in water, and in our first experiments the washing was needlessly prolonged with the view of obtaining a filtrate which would give no colour with alkalies; but this was found impossible, a slight yellow colour being always produced. Neither can hot water, nor water containing glycerine be used, as these speedily dissolve the precipitate; while the use of ether is also inadmissible, owing to a reaction with the lead acetate, which involves the precipitate we wish to retain, and leads to considerable destruction and loss of it by solution in the ether. The ether, moreover, will not pass through the filter, but requires to be shaken up with the precipitate. But these procedures were found to be unnecessary, and the precipitate, simply washed as above, is next suspended in water, decomposed by H_2S, and the resulting solution either evaporated *in vacuo* over sulphuric acid, or extracted with a large quantity of ether. In driving off the latter, the last portions must be poured out in very thin

layers on large watch-glasses, and the evaporation conducted at a temperature of 20° to 30° C. In either of these ways we obtain a definite compound, with a marked acid reaction, which crystallises in needles forming stellate groups of various sizes, according to the degree of rapidity with which crystallisation has taken place, and which coalesce to form a complete scale on the surface of the glass. They have a somewhat aromatic odour, and are slightly irritating to the nostrils, and before they have become quite dry are of a yellow colour, but after complete desiccation of an almost greyish tinge. If they be exposed to a temperature of 60° C. or thereby for some time, they assume a darker dull yellow colour, and they even darken somewhat at a considerably lower temperature. The substance does not appear to be essentially altered, however, although darkened, by exposure to a temperature of 40° or 45° C.; and it may easily be crystallised by slow evaporation of its watery solution in the air, but at higher temperatures it shows a tendency to lose its crystalline character, and to become pulverulent, besides changing to a darker hue. The crystals we have obtained have generally been somewhat yellow, and have furnished (at least in a concentrated form) yellow solutions; but the finest and most recent specimens procured have been of an opaque almost milk-white colour, and from this circumstance we would propose to call this body *Uroleucic Acid.*

The substance thus obtained may be further purified by recrystallisation from ether, or by reprecipitation with lead acetate, if this be thought desirable. In this way specimens which have become darker than usual may be partly recovered. The dried crystals of this purified uroleucic acid show a fixed melting point which, as the result of several trials, we have found to be about 133·3° C. They melt into a dark liquid, which boils at a temperature a few degrees higher, but no odour is given off although this be raised to 205° C.

We now made an ultimate organic analysis of this definite compound, which has shown it to be free from nitrogen and rich in carbon, containing, as it does, as many as nine atoms of the latter element. The average percentage of carbon, hydrogen, and oxygen obtained in the last four analyses, which agreed closely with each other, was—

C	=	54·457	per cent.
H	=	4·985	,,
O	=	40·55	,,

On calculation, the lowest formula corresponding to this will be found to be $C_9H_{10}O_5$, the required percentage of the respective elements for which is—

C	=	54·54
H	=	5·05
O	=	40·40

The error in the carbon is therefore ·088 per cent., and in the hydrogen 0·14 per cent. The amount analysed on each occasion was 10 grains, and two of the samples of the acid were prepared by evaporating a watery solution *in vacuo* over sulphuric acid, and the other two by extracting with ether. The above result was corroborated by other evidence, which appeared also to show that the above was really the rational formula of the acid, and that it was monobasic. The atomic weight of $C_9H_{10}O_5$ is 198, and when caustic soda (NaHO, atomic weight 40) was added to a solution of the acid, in the proportion of 40 parts to 198, the latter lost its acid reaction, but not before; while beyond this proportion of soda the liquid became alkaline, and darkened if exposed to the air. To avoid access of air during the combination of the acid and alkali, they were made to unite under a layer of petroleum ether, in which the former is insoluble.

It may here be mentioned that before we had isolated uroleucic acid we analysed the mixture from which it is obtained, and found its composition to correspond closely to the formula $C_8H_{10}O_6$, in which it will be observed that the hydrogen remains the same as in the above.

Uroleucic acid is very soluble in ether and alcohol, 100 parts of the former taking up 20·5, and of the latter 17·7 parts of the acid. The saturated ethereal solution in the specimen examined had a yellow colour, while the alcoholic became brownish, although it again deposited the acid unchanged. The solubility in boiling water was about 5 per cent., in cold about 4; and the acid was also freely soluble in glycerine, but insoluble in chloroform.

The following reactions and properties may be further particularised :—

A ½ per cent. solution gives a deep reddish-brown colour with alkalies, just a little less deep than that yielded by an equal volume of the fresh urine, which must contain 1 in 500 or 600 of the acid. This colour is about five times deeper than that obtained from gallic or tannic acid, and the latter do not give the brown shade, but almost a pure red in comparison. Oxyphenic acid (pyrocatechin), on the other hand, produces three times more colour than uroleucic acid, and this is at first an intense green, and then a brown without any red.

The same solution (½ per cent.) gives with a 1 in 40 solution of ferric chloride a transient green colour, instantly disappearing on diffusion of the two liquids, and incapable of being rendered permanent with any proportions of the reagents. The ferric chloride, however, produces a red colour when a little is dropped on the crystals of uroleucic acid, this again giving place to the transient green when the amount of ferric chloride is increased. Lastly, when the latter is cautiously added to a strong solution of the acid, the evanescent green which first appears gives place on diffusion to a brownish or reddish colour; on further addition of the chloride, the green fades away into a pale yellow, like that of the chloride solution itself.

The same solution gives no precipitate with a saturated solution of neutral lead acetate, and even a 2 per cent. solution only a slight one. The basic acetate throws down a white precipitate, which becomes violet on exposure to the air.

The acid has an extraordinary power of reducing Fehling's solution, even when immensely diluted. It also quickly reduces solutions of mercuric nitrate, silver nitrate, and chromic acid. These are all reduced almost instantaneously by a 2 per cent. solution, and even a solution of only ½ per cent. acts on silver in the cold in a few seconds. In the case of chromic acid there is thrown down a red precipitate, along with the green suboxide of chromium. A ½ per cent. solution instantly decolourises a solution of potassium permanganate, without the aid of hydrochloric acid.

A most interesting fact in connection with the new acid is its

undoubted power of reducing bismuth, as already stated (Löwe's bismuth test solution was used). To be able to do so, however, the solution must be of the strength of ½ per cent. or upwards; and hence the reason why this fact was not previously ascertained, the acid having never been isolated, and the urine not containing a sufficient quantity of it to manifest this reaction.

The crystals of uroleucic acid are instantly acted on and oxidised by nitric acid, with effervescence and evolution of nitrous acid fumes, and a yellow pasty substance is left. This yields to water and ether yellow solutions, from the former of which it is deposited in an apparently amorphous state, but from the latter in acicular and columnar forms. Either of these redissolved in water shows an acid reaction, and becomes slightly darker with alkalies or a drop or two of Fehling's solution; while a larger quantity of the latter turns it green, but there is no reduction of the copper on boiling. It gives a yellow precipitate with both neutral and basic lead acetates, and also with barium hydrate, besides a slight one with lime-water. Ebstein and Müller state that their pyrocatechin was oxidised to oxalic acid by nitric acid, but this does not result from the oxidation of uroleucic acid by the same reagent.

A trace of chlorine turns the crystals of uroleucic acid of a blue colour, and free exposure to the gas bleaches them completely. These blue crystals, however, do not produce a blue solution, but a yellower one than before; and the gas, when passed into a solution of the acid, also renders it more yellow. We lost several preparations of the crystals by their being thus turned blue, and spoiled, by a trace of chlorine in the atmosphere, before the cause was discovered.

A few general statements must suffice with respect to the other constituents of what we have called urrhodinic acid. The aromatic filtrate above referred to, left after removal of the pale precipitate, contains a body having also an acid reaction, and which may be obtained by precipitating with basic lead acetate; or better, (1) by extracting directly with ether, or (2) by removal of lead by H_2S, and subsequent evaporation *in vacuo* over sulphuric acid. By the last method small stellate groups of a bright yellow colour are deposited, the yellow substance, however, being apparently an amorphous deposit on a crystalline

skeleton formed by a different body. Such was found to be the case by treating with ether, which dissolved the yellow ingredient readily, leaving behind a small quantity of white irregular needles, insoluble in this menstruum. The latter body, of which we obtained only $\frac{3}{4}$ of a grain, proved also very sparingly soluble in water; and we will only further remark of this solution, that it gave a bright pink colour with alkali. The ether deposits the pure yellow substance in an amorphous granular form, and the ultimate result is therefore the same as that obtained by extracting the original aromatic filtrate directly with ether, according to the other method already mentioned. This yellow body, when thoroughly dried *in vacuo*, felt hard to the touch, but on afterwards pounding it in a dry mortar it was resolved only into a pasty mass, and it could not be rendered pulverulent, however long it was kept in the vacuum. It never becomes dry in the air, as it melts and turns dark about 30° C., and below this temperature it is always viscid, so that we cannot be sure it does not retain moisture. The dark liquid boils at a low temperature, and is decomposed with the evolution of an intensely disagreeable putrid odour, below the boiling point of water. It forms a varnish-like deposit on porcelain capsules and glasses above 30° C., partly yellow but partly of a dark red colour, according to the degree of heat to which it has been exposed. In these and other respects which might be mentioned, it will be seen to correspond exactly with Bödeker's "alcapton"; the "much brown powder," (with traces of hippuric acid), which he mentions as occurring at the end of his process, and which we have also seen, being derived, as we now know, from the crystalline uroleucic acid. This amorphous body, from its yellow colour, may be distinguished meanwhile by the name of *Uroxanthic Acid.*

This amorphous substance, when rendered alkaline, gives scarcely half as much colour as the crystalline acid does, but the respective tints closely resemble each other. It may be said, generally, that it exercises the same reducing actions as the latter, with the exception that it does not reduce bismuth, while the action on the other substances is less keen and rapid. It also gives the same transient green with ferric chloride, but not the red colour when in excess. Our analysis of this substance

is not yet ready for publication, but enables us to state positively that it contains considerably more oxygen than the crystalline acid.

The dark precipitate yields a body, also with an acid reaction, which by evaporation *in vacuo* over sulphuric acid, or at a low temperature in the hot-water oven, is obtained as a powder, or in the form of irregular branching crystals, but at a higher temperature in the air as a dark, oily-looking liquid. Its solution also gives a transient green colouration with ferric chloride, but not a red colour in excess like uroleucic acid. A strong solution even does not reduce bismuth, and it does not give much colour with alkalies, a solution of 2 per cent. or so only becoming brown; nevertheless, it manifests all the reducing actions already mentioned, only these are not so keen. It is very sparingly soluble in ether, which renders it tough and viscid, but takes up a small quantity, which is again deposited from it in stellate groups of partly broken, somewhat pulverulent, needles of a yellowish-brown colour, having a general resemblance in form, however, to those of the first acid. Indeed, if we decompose the dark and pale precipitates together by H_2S, and extract with ether, we get the crystalline formation of uroleucic acid, but now of a rich yellow colour.

None of the three compounds above noticed have been found to have any action on polarised light, but we may repeat our observations on this point with the more perfectly isolated bodies recently obtained.

The fourth constituent of our original mixture, the insoluble powder, exists in very small quantity in freshly-prepared samples, and its formation appears to depend on exposure to air and moisture. It dissolves in ether with a red, and in alkalies with a brown colour, and the latter solution does not reduce Fehling's copper test if the powder has been thoroughly separated from the other ingredients.

Our latest observations appear to show that both the insoluble powder and the acid which forms the dark precipitate do not exist in the urine as such, but are produced in the course of the analysis or after exposure to the air. Quite recently we found that by acidulating the urine with hydrochloric acid beforehand none of the red body was obtained, and very little insoluble

powder, which, moreover, had only a yellow colour, and dissolved easily in boiling water. At the same time the yield of uroleucic acid was increased, and as much as 20 grains was obtained from 33 ounces of urine. This may seem surprising after the statement in my previous paper that urrhodinic acid decomposes during the evaporation of its watery solution, and indeed it was a surprise to ourselves. But that error arose chiefly from the result of Bödeker's process, the final evaporation in which yielded little but powder and the amorphous "alcapton." Further, we have now evaporated down solutions of the free acid, both slowly over the water-bath and by boiling, and also solutions of the neutral combination of the acid with sodium, and have found that the body yielding the dark precipitate may be obtained by the latter of these two procedures, although it has not in all cases been identical in shade with that obtained from the urine. Even as derived from the latter, moreover, it has also varied somewhat in depth of colour in specimens prepared at different times. Neither of these two procedures, however, has yielded any of the amorphous aromatic substance, which we therefore conclude must occur as such in the fresh urine, although it probably owes its origin in the animal system to the same source.

It will be allowed that the foregoing account quite agrees with and explains the chief results of Bödeker, whose alcapton was at all events one of the bodies actually existing in the urine, although he did not isolate it in a pure state. It is remarkable that the urine should contain two substances differing so much from each other in certain respects, and yet with such a family likeness in their reactions; and it is clear how this circumstance, coupled with the transformations which one of them may undergo, has increased the difficulty of isolating and identifying them. It has generally been believed by authorities that the urine in Ebstein and Müller's case must have been of the same character as in that of Bödeker, although these investigators lay stress on two points as proving a difference, viz., that their pyrocatechin did not reduce silver nitrate in the cold without the aid of alkali, and had no reducing power on chromic acid at all. But if we evaporate down the fresh urine without acidulation and extract with ether, we can get precisely

the same result. If we shake up the unconcentrated fresh urine with ether we get a small quantity of the crystalline and amorphous acids which crystallises readily in stellate groups, as if one substance only. But after evaporation the result is quite different, and varies according to the temperature to which the liquid has been exposed, and the extent to which the concentration is carried. We have repeatedly evaporated down 40 ounces of urine to determine this point. When this has been reduced to about an eighth the other deposits the two bodies on a watch-glass generally in four concentric zones, the central one consisting of a darkish powder, which has scarcely any reducing power; the second and fourth formed mainly by granular masses of the amorphous substance; and the third zone (between the two latter) containing a few brown circular crystals representing the crystalline acid. When the concentration is carried on till the urine is reduced to a syrup the ether may deposit nothing but an oily liquid in the centre of the glass, round which a few very fine stellate groups may form slowly in the course of a day or two. This deposit has often an alliaceous odour, and may have so far lost its characteristic properties that it cannot reduce nitrate of silver, and chromic acid, if at all, only after prolonged boiling. Further, this deposit gives a pronounced green with alkalies before becoming reddish-brown, and Ebstein and Müller expressly mention this fact, although the urine in their case, as in other cases of alcaptonuria, did not do so. It may be finally noticed that the transient green colour observed by Professor Hartley in Professor Smith's case, with the crystals isolated by him, when treated with ferric chloride, was the characteristic reaction of uroleucic acid; whereas protocatechuic acid would have produced an intense and permanent green. The urine in alcaptonuria does not contain a trace of pyrocatechin or protocatechuic acid.

NOTES ON THE LIMB MYOLOGY OF *PROCYON CANCRIVORUS* AND OF THE *URSIDÆ*. By

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THE following notes on the myology of the limbs of Procyon were made in the course of a series of dissections of the muscular system of the Carnivora. As I have been able to compare my observations on this animal with the accounts given by other writers[1] of the myology of the forms generally regarded as standing nearest to it, the subject seemed to be sufficiently complete to warrant a short note of the group.

I have abstained from any lengthy comments or references, partly from a desire to make this paper as brief as possible, and partly because I hope to publish in time a more detailed account of the musculature of the Carnivora, in which this note will be embodied.

Muscles of Back and Shoulder.—The dorsi-humeral panniculus is very extensive. It commences posteriorly on either side by a slip attached to the fascia covering the root of the tail, covers the latissimus dorsi, passes round its outer border, and is there continuous with the abdominal panniculus, forming with it the brachio-lateral subcutaneous muscle of some authors. The combined sheet is inserted into the humerus under the deepest stratum of the pectoral muscle. A somewhat similar arrangement is found in Ursus. Trapezius consists of two portions—the first or occipito-nuchal arising from the occipital bone and upper part of the ligamentum nuchæ, in close relation to the lower part; passing backwards it is joined by the levator claviculæ arising from the mastoid process. Below the point of junction is a transverse tendinous intersection, underneath which, but lying in the fascia and unconnected with any muscle,

[1] (1) "Short Notes on the Myology of the American Black Bear (*Ursus Americanus*)," by Professor J. Shepherd, *Jour. of Anat. and Phys.*, vol. xviii. p. 103; (2) "On the Myology of the Limbs of the Kinkajou (*Cercoleptes caudivolvus*)," by J. Beswick-Perrin, *Proc. Zool. Soc.*, 1871, p. 547; (3) "Notes on the Myology of the Coati-mondi (*Nasua narica* and *N. fusca*)," by H. W. Mackintosh, B.A., *Proc. Roy. Irish Acad.*, vol. ii. ser. ii., No. 1, p. 48.

is a minute spicule of bone, the clavicle. Below this, the muscle which corresponds here to the clavicular part of the deltoid is attached to the humerus, in common with part of the pectoral, at the deltoid tubercle. The lower portion of trapezius, which is connected with the remainder of the lig. nuchæ and some of the dorsal vertebræ, is inserted as usual and forms one single sheet. This portion at its outer border is joined by the levator scapulæ, which arises from the anterior surface of the transverse process of the atlas, passes under the first part of the trapezius and separates it from the second. In Ursus the anterior part of the trapezius receives a slip from sterno-mastoid, levator claviculæ joins it on its deep surface at the tendinous intersection, and levator scapulæ is quite distinct from the second part of trapezius at their insertion. In Cercoleptes the levator claviculæ arises from the digastric groove, and is inserted into the rudimentary clavicle and into the anterior part of trapezius. The lower trapezii of opposite sides are connected with one another by an aponeurosis but have no bony attachment. In Nasua the trapezius consists of three separate portions—scapularis superior and inferior and clavicularis, which in *N. fusca* is joined by cleido-mastoid and is attached to clavicle, brachialis anticus and humerus. Latissimus dorsi consists of two parts, an anterior which is much the larger, gives off dorsi-epitrochlear and is inserted as usual, and a posterior connected with the former only at its origin, which joins the dorsi-humeral muscle and is inserted with it. In Ursus there is not this division, but the muscle gives off dorsi-epitrochlearis and a slip to the dorsi-humeral. In Cercoleptes one part is joined with teres major and inserted as usual, a second joined by part of dorsi-humeralis is connected with the pectorals, and from the former comes dorsi-epitrochlearis, which receives slips from dorsi-humeralis and teres major. The connection between dorsi-epitrochlearis and teres major is present in *Nasua narica*, wanting in *N. fusca*. The pectoral muscles consist of (1) a portion arising from the manubrium and part of gladiolus, which expands as it passes outwards, and is inserted in close connection with the superficial part of the deltoid; (2) a deeper narrow portion, arising from the manubrium and first costal cartilage and inserted into the capsule of the shoulder-joint; and (3) a portion arising from

the whole of the sternum below 1, and from the costal cartilages and inserted into the shaft of the humerus below 2. The abdomino-humeral panniculus, which arises from the whole of the anterior part of the abdomen, lies close below this last part but unconnected with it, and is inserted with dorsi humeralis and the smaller part of latissimus dorsi beneath it. Shepherd describes in Ursus a muscle similar to 2 as P. minor, but it does not correspond with the muscle known by that name in human anatomy, but with one occasionally present in man, and called pectoralis minimus; 1 and 3 are joined inseparably at their origin in Ursus but soon divide. In Cercoleptes 2 is wanting, 1 arises from anterior half of sternum, and 2–7 ribs, and 3 beneath it from 2–7 ribs, passing to the great tuberosity of the humerus, the capsule of the shoulder-joint, and the coracoid process. A lower portion arises from 7–10 ribs meso- and xiphi- sternum, and is inserted with dorsi humeralis. Nasua has 2, "presterno-humeralis," 1 arises from the whole of the sternum, and 3 deeper from side of sternum opposite first six ribs. The lower abdominal part, P. quartus, arises in this animal, from the cartilages of the lower ribs and the fascia over them. Deltoid consists of the superficial part already described, and a deep, quite separate, acromio-humeral. This portion joins the superficial in Ursus. The occipital and other rhomboids form a single muscle, as is the case in Cercoleptes and Nasua. Shepherd describes R. major and minor as in man, but Macalister[1] says that Ursus has an occipital rhomboid also. Levator anguli scapulæ and serratus magnus form a single muscular sheet in all.

Muscles of the Arm.—There is only a coraco-brachialis brevis which commences by a very long tendon, and biceps has no short head. In Nasua the condition of these muscles is similar. Ursus and Cercoleptes have coraco-brachialis brevis and longus and a two-headed biceps. Supra- and infra- spinatus, teres minor, and subscapularis have no special points of interest. Teres minor is unsegmented from infraspinatus in Ursus and Cercoleptes. Teres major gives a slip to dorsi-epitrochlearis in Ursus and Nasua.

Triceps consists of longus arising in the usual situation,

[1] *Morphology of Vertebrates*, p. 262.

externus arising from the neck of the humerus, internus arising from below the insertion of coraco-brachialis for a short distance, and anconeus arising beneath these but separate from them, and also having an attachment to the external condyle. In Ursus, longus arises from the whole of the axillary border of the scapula, and anconeus from the back of the external condyle, a fourth head of triceps arising just above it and joining the common tendon. Anconeus is unsegmented from internus in Cercoleptes. In *Nasua narica* the anconei are united to biceps; in *N. fusca* anconeus internus arises from the supra-condyloid process.

Muscles of the Fore-Arm and Hand.—Pronator radii teres has a single origin and normal insertion. In Ursus and *Nasua narica* this last extends to the end of the radius. Palmaris longus commences as a single muscle but soon divides; the larger part going over the annular ligament becomes expanded, and ends in slips for the three central digits; the smaller part is inserted into the pisiform. In Ursus this muscle is absent. Flexor carpi ulnaris is double, one portion coming from the common tendon, the second from the inner side of the olecranon, and both being inserted into the pisiform. There is a similar arrangement in Ursus. In Cercoleptes Mr Perrin describes a muscle as "palmaris longus internus," which arises from the fascia covering F. carpi ulnaris. This is doubtless a second part of the last-mentioned muscle; it is supplied by the ulnar nerve, as he points out. Flexor sublimis digitorum consists of two parts—(1) smaller, arises from the common tendon, crosses the deeper part, and joins that part of F. profundus which goes to pollex; (2) arises beneath the first from the common tendon, gives off from its deep surface a tendon which joins F. profundus in the palm, and then breaks up into slender perforated tendons for the three central digits. In Ursus the muscle divides into three slips:—(1) gives perforated tendons to index, medius, and annularis; (2) gives perforated tendons to minimus, and a slip to pisiform; (3) passes to pollex. In Cercoleptes the muscle divides into two lateral portions, which join profundus, and a mesial which splits into four tendons,—one deep to profundus, three superficial perforated for the three central digits. In Nasua, four perforated tendons are given to the four inner digits. In connec-

tion with this muscle must be mentioned a small muscle arising in Procyon from the annular ligament and pisiform bone, and inserted into the sheath of the flexor profundus, but not perforated by it, at the base of the proximal phalanx. A similar muscle is described in Cercoleptes, but is perforated by the deep flexor. In these four forms we have in the relations of the superficial flexor of minimus a very interesting series of stages of regression, as I read the facts. In Nasua the perforated tendon comes as usual from sublimis; in Ursus it does so also, but gives a slip to pisiform as well. In Cercoleptes the proximal portion of the muscle has disappeared, but the distal arising from the pisiform is still perforated. Finally, in Procyon it no longer has any perforation, but is only connected with the sheath of the tendon of the deeper muscle.

Flexor profundus, besides the portions mentioned above, receives a perfectly distinct adjunct, arising with but separate from sublimis; this lies between the two muscles joining the deeper in the palm of the hand. The great mass of the deep muscle arises in two portions, which subsequently unite from the front of the radius of the ulna. Ursus also has a portion arising from the internal condyle. Pronator quadratus covers two-thirds of the length of the bones of the fore-arm in Procyon and Cercoleptes; in the others it is disposed as in man.

The superficial extensor of the digits arises with the first part of the deep, and passes to the four inner digits. The deep extensor consists of two parts; (1) arises with the superficial, and lies on its ulnar side for a short distance, it then passes beneath it and ends in tendons for minimus, annularis, and medius; (2) arises from the proximal part of the radial border of the ulnar, and ends in two tendons, one of which goes to index, the second representing extensor secundi pollicis. Extensor ossis metacarpi pollicis is a very strong muscle. In the other animals, as to the deep extensor, in Ursus 1 is much larger than the superficial muscle, and 2 goes only to pollex, index having no deep extensor. *Nasua narica* has separate extensores minimi, annularis et medii, and indicis et pollicis. In *Nasua fusca* medius gets a slip from both parts of the deep extensor. Supinator brevis has no ulnar attachment, but arises from the orbicular ligament of the radius. In Ursus it arises also from

the external condyle, but not from the ulna. In the hand Procyon has superficial adductors for pollex, index, and minimus, as have the other animals. Pollex has abductor, opponens, and flexor brevis; minimus has an abductor, and flexor brevis. The three central digits have each a pair of interossei.

Muscles of the Thigh.—Gluteus maximus is thin but fairly extensive, arising by a thin, strong aponeurosis from the greater part of the iliac crest, and being inserted as usual. Gluteus medius is very large and strong, and arises from the upper two-thirds of the outer surface of the ilium. It is more or less continuous with pyriformis in Cercoleptes. Gluteus minimus consists of two imperfectly separated portions; the anterior, which I look upon as gluteus quartus, arises from the anterior edge of the ilium below sartorius and tensor vaginæ femoris, the posterior and smaller part taking origin from the lower part of the ilium below medius; the latter is partly inserted with the former and partly beneath it to the great trochanter. Quartus and minimus are fused in *Nasua narica;* there is no mention of the former in the other forms. Biceps femoris arises altogether from the tuber ischii, and soon expands into a large sheet of muscle, which is attached (1) to the whole of the fascia of the thigh; (2) to the outer side of the patella; (3) to the front of the tibia by an aponeurosis more tendinous in appearance than the rest of its connections; and (4) to the fascia of the leg nearly as far down as the ankle. In Ursus it is also inserted by a round tendon into the os calcis, and there is an accessorius. In Cercoleptes, biceps has a caudal head. In *Nasua narica,* accessorius arises with agitator caudæ, and is inserted with biceps; in *Nasua fusca* it arises with the caudal head of semitendinosus, and is inserted into the middle of the fibula.

Semitendinosus arises by two heads—one from the tuber ischii, the other from the upper caudal vertebræ; it is a small muscle, and is inserted beneath the gracilis. Ursus has only the ischial head, Nasua has both; in Cercoleptes the muscle is large and bicipital, agitator caudæ arising with its caudal head, and is fused with it as far as the junction with the ischial portion; Nasua has a separate agitator caudæ; but this muscle was not

present in Procyon,[1] unless represented by the caudal head of semitendinosus.

Semimembranosus arises from the tuberosity and adjacent part of the ramus of the ischium, and is very closely connected with, though separate from, the adductor sheet of muscle; it is inserted (1) into the inner side of the tibia, beneath the internal lateral ligament, and (2) into the inner condyle of the femur. In Ursus it is described as consisting of two parts, one inserted into the tibia, the other and larger joining the adductor.

Sartorius is a large muscle, arising from below the anterior superior spine of the ilium, and being chiefly inserted by a strong aponeurosis into the anterior and inner parts of the patella. It also sends down a tongue-like process of muscular fibres on the inner side of the patella, the tendon of which is attached to the tibia above that of the gracilis. Tensor vaginæ femoris is a strong and separate muscle attached as usual. Gracilis forms a thin but extensive sheet arising from the rami of the pubes and ischium, and thus curving round the other muscles above; it is inserted by a flat tendon into the middle third of the anterior surface of the tibia. Pectineus arises from the very prominent ileo-pectineal ridge, and is inserted as usual. The remaining adductors are two in number, (1) a small muscle, arising partly beneath the pectineus and partly internal to it from the front of the pubes as far as the symphisis, it is inserted behind the pectineus; (2) an exceedingly large sheet of muscle, arising under cover of the gracilis from nearly the whole of the descending ramus of the pubes and the anterior part of its body, and from the ramus of the ischium, and inserted into the posterior part of the femur from a short distance below the lesser trochanter to the lower end, and into the internal condyle. Besides this last-mentioned muscle, Shepherd describes a small adductor "a narrow ribbon-shaped muscle, which arises from the tuberosity of the ischium in common with the semimembranosus, and is inserted into the upper part of the internal condyle of the femur and adductor tubercle; a little before its insertion it joins the greater portion." I am inclined to look

[1] Macalister, *Morph. of Vert. Animals*, p. 263, says that the *Procyonidæ* have a separate agitator caudæ muscle, but it did not exist as an isolated muscle on either side in my specimen.

upon this muscle as more properly belonging to the semimembranosus than to the adductor, though, of course, the connection between these two muscles is very intimate. Cercoleptes and Nasua have each three adductores. Quadratus femoris is a large and quite separate muscle.

There is a strong psoas parvus in all the forms, and ilio-psoas presents no special points of interest. The same remark applies to the two obturator muscles; the gemelli are very large and distinct. Pyriformis is also well developed and quite distinct, some of its fibres arising outside the pelvis from the transverse processes of the caudal vertebræ. There is a single-headed rectus, and the remaining parts of the quadriceps are as usual.

Muscles of the Leg and Foot.—The two heads of gastrocnemius are separable in the greater part of the leg, there is no separate plantaris, and soleus has only a fibular origin. The combined tendon is partly inserted into the lower portion of the posterior part of the os calcis, a bursa intervening between the tendon and the bone. The superficial part of the tendon, however, which is here separated from the deep by a second bursa, passes over the os calcis, forming a kind of hood-shaped aponeurosis, from which in the sole of the foot arises the short flexor of the toes. Ursus is described by Shepherd as having a three-headed gastrocnemius, the outer of which he looks upon as representing plantaris; all three are attached only to the os calcis. Cercoleptes has a large plantaris, the tendon of which passes into the sole of the foot, forms the plantar fascia, and is closely associated with the flexor brevis, a similar condition existing in Nasua. Popliteus is a large, strong muscle.

Flexor tibialis arises from the upper third of the tibia, from the head of the fibula, and from the fascia overlying tibialis posticus. Flexor fibularis, which is much larger, arises from the fibula and adjacent fasciæ. The tendons of these muscles unite in the sole, and give slips to the four outer toes. Flexor accessorius arises from the inner side of the os calcis, turns round this bone into the sole of the foot, crosses the combined tendons of the long flexors with which it is slightly connected, and passes joined by a slip from the combined tendon to the hallux. From its side and from the combined flexor tendon spring two small muscular bellies, which end in slender tendons passing

severally to those of the flexor brevis which go to the 2nd and 3rd digits. Flexor brevis arises, as has been stated, from that part of the tendo Achillis which passes over the heel, and gives perforated tendons to the four outer toes. As regards the flexor group in the other forms, accessorius in Ursus passes directly into the combined tendon; in Cercoleptes, brevis supplies tendons only to 2, 3, and 4 digits, each of these tendons receiving a fleshy slip from accessorius, the remainder of which joins the combined tendon. Tibialis posticus has a small muscular belly and a long tendon inserted as usual. Extensor longus digitorum gives tendons only to the three outer toes; extensor brevis, which is a well-developed muscle, gives tendons to the four inner. Extensor longus hallucis is small. Peroneus longus is, as usual; the tendon of brevis passes behind that of longus, runs along the side of the foot, and is inserted into the base of the middle phalanx of the fifth toe. There is no separate peroneus quinti. This last muscle is present in all the other forms.

Tibialis anticus is a large muscle.

Hallux has an adductor, abductor, and flexor brevis. The first muscle is described by Perrin in Cercoleptes as "obliquus tarsi." Minimus has adductor, flexor brevis, and an abductor inserted into the spur at the base of the metatarsal bone. Each of the other digits has a pair of interossei.

ON THE ANATOMY OF *HYÆNA STRIATA*. By ALFRED H. YOUNG, M.B., F.R.C.S., and ARTHUR ROBINSON, M.B., *The Owens College, Manchester.*

PART I.

THE observations of Reimann, Rudolphi,[1] Daubenton,[2] Hunter,[3] Meckel,[4] Cuvier,[5] and others have already made us fairly well acquainted with the anatomy of the soft parts of *Hyæna striata*, and but little is wanting to complete their descriptions.

In view, however, of more recent observations on the structural peculiarities of the nearest allies of *H. striata*, it seemed advisable to make a further examination of the soft parts of the species, and to place the result of this on record, in the hope that by so doing the anatomy of the group might be made more complete.

The opportunity for making such an examination was afforded by the kindness of Messrs J. Jennison & Co., of the Zoological Gardens, Manchester, to whom we desire to express our indebtedness. The specimen placed at our disposal was a well-developed female, fresh, and in good condition. It measured 3 feet 9½ inches from the tip of the nose to the root of the tail.

Of the recent observations to which allusion has been made, we refer, in particular, to those on *Hyæna crocuta* by Watson and Young,[6] those on *Hyæna brunnea* by Murie,[7] those on *Proteles* by Flower[8] and by Watson,[9] and those on *Viverra civetta* by one of ourselves.[10] To these, as well as to the writings of Meckel, reference is frequently made in the following description of *H. striata*, and in order to avoid needless repetition, we wish it to be understood that, except when otherwise specified, they

[1] *De Hyæna*, Berol, 1811.
[2] Buffon, *Histoire Naturelle*, tom. ix.
[3] *Essays and Observations*, edited by Owen, 1861, vol. ii.
[4] *Anatomie Comparée.*
[5] *Leçons d'Anatomie Comp.*
[6] *Proc. Zool. Soc.*, 1879, p. 79.
[7] *Trans. Zool. Soc.*, vol. vii. p. 503.
[8] *Proc. Zool. Soc.*, 1869, p. 474.
[9] *Proc. Zool. Soc.*, 1882, p. 579.
[10] *Jour. Anat. and Phys.*, vol. xiv. p. 166.

are to be regarded as our authority in all comparative observations; and that, further, we have followed very closely the plan of description adopted in the account of the Spotted Hyæna.[1]

VISCERA.

Digestive Organs.

Tongue.—The tongue of *H. striata*, both as regards its form and the arrangement of its papillæ, agrees with that of *H. crocuta.* The fungiform papillæ are, however, not so numerous as in the latter species. Daubenton[2] affirms the existence of four circumvallate papillæ in the Striped Hyæna; in our specimen, however, there are only two, which is apparently the usual number in Hyænidæ.[3]

In *H. crocuta* the soft palate is short, and there is no trace of an uvula. In *H. striata* the soft palate is longer, and a short uvula exists. The azygos uvulæ muscles are strong and well defined.

The hyoid bone is composed of the usual elements, a central portion or basi-hyal, with anterior and posterior cornua. The anterior cornua are segmented into cerato-, epi-, and stylo-hyal elements, whilst the posterior cornua are formed by the thyrohyals.

Muscles of the Tongue and Hyoid Bone.—The hyoid bone is attached to the lower jaw by *mylo-hyoid* and *genio-hyoid* muscles. The mylo-hyoid forms the diaphragm of the mouth. The genio-hyoid muscles are distinct at their attachment to the body of the hyoid bone, but are fused at their origin from the back of the symphysis.

Two muscles pass between the tongue and hyoid bone on each side, a strong *hyo-glossus* and a small *cerato-glossus.* The *sterno-hyoid* and *sterno-thyroid* muscles have a common origin from the thoracic surface of the anterior portion of the sternum; the former are inserted on the basi-hyal, the latter on the sides of the thyroid cartilage.

The *thyro-hyoid* passes from the thyroid cartilage to the basihyal.

[1] *Proc. Zool. Soc.*, 1879, p. 79.

[2] Buffon, *Histoire Naturelle*, vol. ix. p. 129.

[3] Meckel, *Anat. Comp.*, vol. viii. p. 685, and Reimann, *De Hyæna*, Berol, 1811, p. 15.

The *stylo-hyoid* is absent, as in *H. crocuta, Viverra, Proteles*, Wolf, and Dog. Meckel affirms its presence in *H. striata.*

There are strong *inter-hyoid* muscles which unite the thyrohyals to the basi-, epi-, and cerato-hyals.

The epiglottis is attached to the cerato-hyals by distinct muscular bundles.

The *stylo-glossi* are strong, and by their union anteriorly form the tip of the tongue.

The *genio-glossi* are flat triangular muscles attached by their apices to the back of the symphysis. Their bases were embedded in the mesial portion of the tongue.

Muscles of Pharynx and Soft Palate.—Three constrictor muscles surround the walls of the pharynx; the superior and middle are partially separated from each other by the strong stylo-pharyngei.

The palato-pharyngei are strong; they are united in the middle line over the azygos uvulæ, and are lost below on the sides of the pharynx.

The *œsophagus* possesses strong muscular walls; the mucous coat is thick, dense, and longitudinally plicated.

The *stomach,* which measures when empty 9¾ inches in length and 7½ inches in its greatest breadth, corresponds almost exactly to that of *H. crocuta,* and with the figure given by Daubenton. Its mucous membrane, however, is not so markedly divided into the three portions described and figured in *H. crocuta,* and which was first observed by Flower in *Proteles.*

We could not distinguish any trace of the central tendon described by Murie in *H. brunnea* and noted in *H. crocuta.* The whole organ is somewhat more globular than in the Spotted Hyæna, and a better marked though still shallow cardiac *cul de sac* exists. The pyloric constriction is annular in form.

The *small intestine* measures 21 feet 7 inches in length.[1] Its diameter is greatest at the duodenum, below which it gradually diminishes down to its termination. There are none of the constrictions which exist in the Spotted Hyæna. The mucuous membrance is smooth and devoid of valvulæ conniventes. We noted eight Peyerian patches. The same number obtains in *H. crocuta* and in *Proteles.*

[1] See table of relative lengths of this and other species, *Proc. Zool. Soc.*, 1879, p. 84.

Great Intestine.—The cæcum measures 7½ inches. The total length of the great intestine down to the anus and including the cæcum is 3 feet 4½ inches. (See Table, *op. cit.*)

The *liver* and *pancreas* agree with the same organs in *H. crocuta.*

The *spleen*, prismatic and elongated, is somewhat enlarged and bent at one extremity. Its surfaces and margins are smooth. It measures 9½ inches in length and 2¼ inches in its greatest breadth.

The Larynx.—The cartilaginous elements of the larynx include a spade-shaped epiglottis, rounded at its free apex and broadened out basally. It is attached by three folds of mucous membrane to the tongue, and from each outer border a fold of mucous membrane passes backwards to be lost on the surface of the crico-arytenoid muscle, where the mucous membrane is separated from the muscular fascia by a network of venous spaces.

The thyroid cartilage is attached by its anterior cornua to the thyro-hyal elements of the hyoid bone. Its posterior cornua are articulated with the sides of the cricoid cartilage.

The cricoid cartilage, which has the usual signet-ring shape, is surmounted by two pyramidal arytenoid cartilages.

Mayer[1] affirms the absence of false vocal cords in *H. striata.* In our specimen they exist as distinct but lax folds of mucous membrane continuous with each other ventrally. They pass from the anterior margin of the thyroid cartilage to the arytenoid cartilages, just below their apices. It is impossible to bring these cords into contact with each other by altering the position of the laryngeal cartilages; an oval space 1 inch long and a quarter of an inch wide always intervenes. A small fossa separates the true and false vocal cords, as in Carnivora generally.[2] Beyond this there is no laryngeal sac or sinus. The comparatively rudimentary condition of the false cords, and the fact that they cannot be approximated so as to come into contact with each other renders them useless so far as the closure of the glottis during expiration is concerned.

[1] *Nova Acta Acad. Naturæ Curios.*, vol. xxiii., 1851, p. 694.

[2] Brunton and Cash, "The Valvular Action of the Larynx," *Jour. Anat. and Phys.*, vol. xvii. p. 367.

According to Wyllie[1] this is the chief function of the false vocal ends.

The true vocal cords are situated in the edge of somewhat rounded folds of mucous membrane, which extend across the larynx; these folds are due to the projection of the thyro-arytenoid muscles, and disappear when the muscles are removed, each true cord being then more distinctly visible as a flat fibrous band, extending from the angle of the thyroid cartilage to the vocal process of the arytenoid cartilage.

Muscles of Larynx.—The *crico-thyroid* is a strong and well-developed muscle. It has the usual attachments, and consists, as in man, of two portions, straight and oblique.

The *crico-arytenoideus posticus* arises from the whole of one half of the dorsal surface of the cricoid cartilage, and is inserted into the muscular angle of the arytenoid.

The *crico-arytenoideus lateralis* springs from the anterior border of its own half of the cricoid cartilage and passes to the muscular process of the arytenoid cartilage, where it is inserted ventrally to the crico-arytenoideus posticus and external to the thyro-arytenoideus and the arytenoideus.

The *arytenoideus* passes from the muscular angle of the arytenoid cartilage, where it is attached internal to the crico-arytenoids and dorsal to the thyro-arytenoideus, across the middle line, where it decussates with its fellow-muscle to the opposite posterior epiglottic fold. It has no attachment to the opposite arytenoid cartilage.

The *thyro-arytenoideus* is not divisible into internal and external portions. The muscular fibres, which are attached dorsally to the external surface of the arytenoid cartilage and ventrally to the thyroid cartilage and to the ventral fourth of the true vocal cords, are so folded upon themselves that those most external at their origin are most internal at their insertion.

The Lungs.—From the descriptions of the lungs of different specimens of *H. striata*, it seems probable either that the number of lobes found in these organs is liable to variation, or else that differences of opinion exist as to the exact constitution of a lobe. Meckel states that the lungs of *H. striata* are com-

[1] *Edinburgh Medical Journal*, Sept. 1866.

posed of seven lobes, four belonging to the right side and three to the left, whilst Daubenton affirms the existence of four lobes in the right lung and two in the left, the anterior lobe of the left lung being subdivided by a deep fissure.[1] In our specimen the right lung consists of three portions, of which the anterior and internal are, according to Aeby's definition,[2] to be considered as lobes, and the posterior part as the remaining undivided portion of the lung. On the left side there is only one separate lobe, which is placed anteriorly and presents a slight notch in its ventral border, this notch being the only representative of the deep fissure described by Daubenton. The remaining posterior portion of this lung is undivided. The lungs of *H. crocuta* are more subdivided than is the case in *H. striata*. Watson and Young described in their specimen six lobes on the right side and three on the left. Watson[3] subsequently examined another specimen and found five lobes on the right side and three on the left, and it is worthy of note that this second specimen was older than the one previously examined, and that the reduction of the number of lobes was, in Watson's opinion, due to fusion.

In our account of the lungs of *H. striata* we adopt the method of description proposed by Aeby in his elaborate monograph, *Der Bronchialbaum der Säugethiere und des Menschen*, Leipzig, 1880; we may therefore be permitted to refer briefly to the opinions Aeby advances.

Opposing the old idea that the bronchial tubes, as they pass into the lung, divide dichotomously, Aeby demonstrates that each tube forms an axial stem in the lung substance from which branches are given off in definite directions. These branches he divides into "primary" and "accessory," deeming the latter to be, in reality, subdivisions of the primary branches which have changed their position and have become secondarily implanted on the axial bronchus.

The primary branches are divided into two sets, the pulmonary artery as it crosses the axial bronchial tube serving as

[1] *Loc. cit.*

[2] "Ein wirklicher Lappen stutzt sich auf nie mehr als einen einzigen Seitenbronchus und schliesst namentlich auch keinen Theil des Stammbronchus ein."

[3] *Proc. Zool. Soc.*, 1881, p. 520.

the boundary line between the two. All the branches given off from the main bronchus in front of[1] the pulmonary artery Aeby calls eparterial; all those behind the pulmonary artery he designates hyparterial.

The hyparterial bronchi rise from the outer surface of the stem bronchus and pass in two directions, some dorsally, others ventrally; and Aeby therefore classifies them as dorsal and ventral hyparterial bronchi. The pulmonary artery, as it passes backwards, lies on the outer face of the axial bronchus between the dorsal and ventral branches.

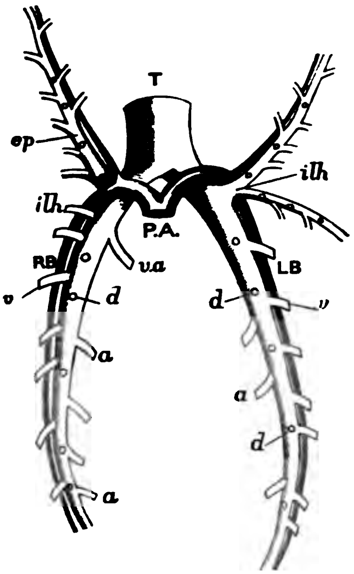

FIG. 1.—The bronchial tubes and their main branches seen from the front. The anterior walls of the tubes are supposed to be removed to show the relative positions of the main branches at their origins. P.A., pulmonary artery; T, trachea; RB, right bronchus; LB, left bronchus; *v*, ventral branches; *d*, dorsal branches; *a*, accessory branches; *ep*, eparterial branch; *ilh*, first lateral hyparterial; *v.a.*, first ventral accessory (right).

Aeby further states that smaller and more irregular branches arise from the inner face of the axial bronchus, some approaching

[1] It must be noted that we are speaking of quadrupeds, and that therefore term "anterior" is synonymous with the term "above," as used by the n anatomist.

the ventral branches, others the dorsal, and these are the bronchi which he terms accessory.

In *H. striata* (fig. 1) the right main bronchus gives off one eparterial and seventeen hyparterial branches; of the latter seven are ventral and five dorsal, whilst five are accessory. The left bronchus gives no eparterial branch, but there are sixteen hyparterial branches, eight being ventral, five dorsal, and three accessory. Aeby maintains that there is a close correspondence between the branches given off by the two axial stems, and he finds that the lobes of the lungs, associated with the various branches, are, speaking generally, developed from before backwards, and that the branches most commonly associated with separate lobes are the eparterial, when present, the first ventral hyparterial on both sides, and occasionally the other ventral hyparterial branches. The dorsal hyparterial branches are never associated with separate lobes, and of the accessory branches one only, the first ventral accessory, sometimes on the right and more rarely on the left side, is enclosed in a separate portion of lung substance. On the supposition that a close correspondence of the branches given off from the axial stem exists, Aeby believes that when, as in *H. striata*, there are two separate lobes on the right side, one being anterior, and supplied by the eparterial bronchus, and only one on the left, also anterior, supplied by the first ventral hyparterial bronchus, the anterior lobes of the two sides do not correspond with each other; and since the anterior lobe on the right side is supplied by a bronchus not found on the left, he believes that the anterior lobe is entirely unrepresented on the latter side.

It has been shown by His[1] that, in the development of the human lung, which possesses on the right side two separate lobes, belonging respectively to the eparterial and first ventral hyparterial bronchi, and on the left only one separated lobe, associated with the first ventral hyparterial branch, that the branching of the first ventral hyparterial bronchus on the left side is more profuse than the corresponding branch on the opposite side, and that in particular it gives off a strong dorsal

[1] *Archiv für Anat. u. Phys. Anat. Abtheil*, 1887.

branch, unrepresented on the right side, which runs upwards and compensates for the absence of the eparterial bronchus.[1]

Our observations on rodents enable us to confirm in them the early appearance of this anteriorly projected offshoot from the first ventral hyparterial branch on the left side; it is a branch entirely absent from the first ventral hyparterial bronchus on the right side. It follows, therefore, from the presence of this offshoot, that in the lungs of man and rodents the anterior portion on the left side, which is supplied by the first ventral hyparterial bronchus, corresponds to the part or parts of the right lung which surround both the eparterial and the first ventral hyparterial branches on the right side.

Our dissection of the lungs of the *H. striata* has brought to light other facts which have an important bearing on the relative values of the eparterial bronchus and the first ventral hyparterial bronchus.

We find that the eparterial bronchus, which is present only on the right side, runs forward in the anterior lobe of the lung of that side to its anterior extremity, and in its course gives off three sets of branches—dorsal, ventral, and internal. Accompanying the bronchus is a branch of the pulmonary artery, which is given off from the right primary division of that vessel as it is crossing the right main bronchus. This arterial branch runs at first along the inner side of the eparterial bronchus, and then passes between the internal and dorsal branches. Aeby considers that the eparterial bronchus represents a combination of a dorsal and a ventral branch of the hyparterial system; but in *H. striata*, this bronchus, both on account of its mode of ramification and the relation of its branches to the accompanying artery, closely simulates the hyparterial portion of the main bronchial stem.

The first ventral hyparterial bronchus on the right side gives off only two sets of branches, and the accompanying arterial

[1] "Damit wird ein Ersatz geschaffen für den eparteriellen Bronchus der rechten Seite."

[2] An examination of the lungs of a fœtal sheep and a young dog showed that the eparterial bronchus gave off only two sets of branches; but the accompanying artery lay not between these but to the inner side of the dorsal set, that is, in the same position as in Hyæna.

branch runs along the outer face of the hyparterial bronchus between these two sets of subdivisions.

On the left side the eparterial bronchus, as such, is absent; but the first ventral hyparterial branch, almost immediately after its origin, divides into two parts, one of which passes ventrally, whilst the other is directed forward. The latter branch gives off a series of subdivisions, which correspond to the ventral, dorsal, and internal branches of the eparterial bronchus on the right side; and they bear the same relation to a branch of the left division of the pulmonary artery, which is given off before that division passes behind the trunk of the first left ventral hyparterial bronchus.

The ventral division of the first left hyparterial bronchus, unlike the first ventral hyparterial branch on the right side, gives off three sets of subdivisions, two of which are separated from each other by the accompanying artery, whilst the third set is represented by only two small branches. Thus it is evident that, in *H. striata*, as in man,[1] the deficiency of the eparterial bronchus on the left side is compensated by a branch from the first ventral hyparterial bronchus; but, further, it is also certain that in this animal the first left hyparterial bronchus is equal in value to the eparterial and first ventral hyparterial of the right side; and that the anterior division of the first left hyparterial bronchus, on account of the number of its sets of subdivisions, and their relation to the accompanying artery, bears the same relation to the main hyparterial stem as does the eparterial bronchus on the right side.

Accessory Bronchi.—In a future paper on the development of the lungs of rodents, it is intended to refer particularly to the secondary position assigned by Aeby to these branches, but at present it is only necessary to deal with the first ventral accessory branch. In *H. striata*, as in many other mammals, this bronchus supplies the azygos lobe. It is of considerable size, being quite as large as the first ventral hyparterial branch, which Aeby regards as its parent stem, and is separated at its origin from the first ventral hyparterial bronchus by a distinct interval.

His has already shown that in the human lung, on account

[1] His., *loc. cit.*

of its early appearance and its position midway between the first and second ventral hyparterial branches, this bronchus has a value similar to that of the other primary branches.

In rodents it is the third branch to appear on the right bronchus, being present before any dorsal branches are developed, and it springs from the main stem at a point beyond the first ventral hyparterial branch.

It appears to us, therefore, that its equal importance with the other primary branehes in some animals is proved by its early and separate origin from the main stem, by its comparatively large extension, and its frequent association with a separate lobe of lung substance. But though we know that in some animals the ontogenesis of this bronchus places it on a similar level with the other primary branches, our researches on a series of mammalian lungs lead us to believe that, as Aeby has suggested, it belongs originally to the first ventral hyparterial branch.

Vascular System.—The heart is short and broad, and only differs from that of the Spotted Hyæna in that there is a distinct though small Eustachian valve. Two main trunks are given from the aortic arch, *e.g.*, (1) an innominate from which the right subclavian and right and left carotids take their rise, and (2) a separate left subclavian. The external and internal iliac arteries arise separately from the abdominal aorta, as in *H. crocuta* and *Proteles.*

Urinary and Generative Organs.

Kidneys.—Each kidney is of ovoid form, and measures 2¾ inches in length, 2 inches in breadth, and 1½ inch in thickness. The organ is enclosed in a strong but easily separable capsule. The surface is smooth, but marked by arborescent veins. Sections show a single large pyramid and papilla, as in *H. crocuta.* In *H. brunnea* Murie found eight cones.

Ureters.—Each of the ureters measures 5½ inches in length. The walls are thick, and the lumen small. The vesical opening is placed close to the orifice of the urethra.

Bladder and Urethra.—The bladder is pyriform in shape, and agrees exactly with the corresponding viscus in *H. crocuta.* The urethra measures 3¾ inches in length; it passes backwards

closely connected with the anterior wall of the vagina, and opens just in front of the latter into a common urogenital canal, which is continued along the under surface of a well-defined clitoris. The urinary and vaginal orifices are separated by a semilunar fold of mucous membrane. A precisely similar fold is described by Watson in *H. crocuta,* as intervening between the opening of the urethra and that of the os uteri into the common canal.[1]

Ovaries.—Each ovary lies, as usual, on the inner face of the broad ligament. It is attached posteriorly to the tip of the cornu uteri by a strong musculo-fibrous ovarian ligament, and anteriorly to the posterior surface of the diaphragm by a diaphragmatic ligament. It lies at the dorsal end of an ovarian sac or pavilion, which, as regards completeness, is intermediate in position between that found in the bitch and in the badger respectively.[2] In the bitch, the whole length of the ovary is exposed; in the badger, it is entirely concealed in the ovarian sac, whilst in *H. striata* the posterior half of the ovary is visible. The ovary is ovoid in form, flattened laterally, and has a smooth surface, thus resembling the corresponding structure in the other species of Hyæna.

The *Fallopian tubes* are 3 inches long; each runs at first forward and ventrally in the outer wall of the ovarian sac, and then suddenly bending on itself in the lower edge of the sac it passes dorsally and ends in a fimbriated orifice, which is placed on the lower edge of the mouth of the ovarian sac.

Uterus.—The uterus is bicornuate. Each horn from its extremity, where the ovarian ligament is attached, to the junction with the opposite horn in the body of the uterus measures 2¾ inches.

The body of the uterus, formed by the junction of the opposite horns, is somewhat flattened but of fairly uniform calibre. Two and a quarter inches below the junction of the cornua there is a somewhat sudden increase in the diameter, and this corresponds to the position of the os uteri and the beginning of the vagina. The fusion of the canals of the uterine cornua is placed internally exactly 1 inch below the junction of the cornua as

[1] *Proc. Zool. Soc.*, 1877, p. 373.

[2] A. Robinson, "The Position and Peritoneal Relations of the Mammalian Ovary," *Jour. of Anat. and Phys.*, vol. xxi.

seen externally; the cavity of the body of the uterus extends 1¼ inch below this. Its mucous membrane is longitudinally rugose. A well-defined os uteri exists.

The *vagina* measures 3 inches in length, and extends from the os uteri down to the common urogenital passage, into which, as already stated, it opens with the urethra, the two orifices being separated by a semilunar fold of mucous membrane, which may be regarded as a hymen.[1] The mucous membrane of the vagina is marked by longitudinal rugæ, except at its lower end.

The *urogenital canal* is 1½ inch long. It extends from the openings of the urethra and vagina, being formed by the junction of these tubes, to the extremity of the clitoris, running on the under surface of the latter and grooving its whole length.

External Organs.—The superficial appearances in the region of the perinæum are much as described by Murie in *H. brunnea.* The opening of the vulva, 1 inch in length, is slit-like or elliptical, and bounded in front by two rounded elevations, which Murie regards as labia majora. Watson concluded that the scrotal pouches of the female *H. crocuta* were the homologues of the labia, though it is to be noted that the greatly elongated clitoris opens anterior to them.

There is a well-defined though short hood-like clitoris, grooved inferiorly by the continuation of the urino-genital canal. It does not project beyond the general surface; viewed from below, the appearance of the organ,[2] both as regards structural arrangements and relations, is exactly like the corresponding parts in *H. crocuta* after parturition, except in respect of size.

The observations of the late Professor Watson[3] on the generative organs of the Spotted Hyæna made us acquainted with the remarkable and unique characters of these structures in the female of that species. So strikingly did the structural peculiarities of this group of organs appear to differ from those of its closest allies, and from the normal mammalian type, that they

[1] The animal had never been pregnant.
[2] *Proc. Zool. Soc.*, 1881, pl. xlix. fig. 3.
[3] *Proc. Zool. Soc.*, 1877, p. 369; 1878, p. 416; 1881, p. 516.

were almost regarded, taken *per se*, as justifying the establishment of a separate genus for the reception of *H. crocuta.*[1]

A comparison, however, of the descriptions given by Professor Watson of these organs in *H. crocuta* with what obtains in *H. striata*, shows that even in respect of the reproductive organs the two species are very similar. Such differences as exist depend entirely on the extent of development of the clitoris and its associated parts.

In *H. crocuta* the clitoris is greatly elongated, and tunnelled along its whole length by a common urino-genital canal, into which open both the urethra and the uterus, or rather the vagina. The clitoris is surrounded by a fold of integument which forms a prepuce, and projects prominently beyond the surface of the abdominal wall. From this circumstance, and also by reason of its size, it so closely resembles the male organ that it is not easily distinguishable from it, at least on superficial examination. The similarity in appearance of the external organs in the male and female Spotted Hyæna is made complete by the existence in the latter of "scrotal eminences" which occupy the position of the testicles in the former.

In the female Striped Hyæna the clitoris is not so greatly elongated, and does not project beyond the surface of the abdominal wall; the integument surrounding and enclosing both clitoris and the external aperture of a common urino-genital canal corresponds to the prepuce of the female *H. crocuta.* Both vagina and urethra open into a common urogenital canal, which grooves the under surface of the clitoris and corresponds to it in length. Clearly this is to be regarded as a greatly elongated vestibule.

In the female of *H. crocuta* which has borne young, the passage of the urogenital canal through the clitoris is ruptured, and so the canal opens below the clitoris, and the lower wall of the canal is formed by the prepuce. The similarity in all respects, except as regards extent of development, between the two species is thus made still more evident. The internal organs are in every respect alike. In the account to which reference has so frequently been made of these structures in

[1] Watson and Young, *Proc. Zool. Soc.*, 1879, p. 106.

H. crocuta, it is stated that the whole of the passage between the junction of the uterine horns and the common urino-genital passage is uterus alone. The semilunar fold which separates the urinary from the genital passages was therefore regarded as indicating the position of the os uteri. Subsequent examination of the same specimen, however, has convinced us that a distinction between vagina and uterus exists in *H. crocuta* as in *H. striata*, and that a well-marked os uteri is present, though in the former there is certainly no such external indication, by alteration of size, of the position of the os such as is present in the latter. In the second of the specimens examined by Professor Watson, he distinguished a small projecting fold of mucous membrane about the middle of the body of the uterus which might be regarded as indicating the position of the os uteri.

Anal Glands and Pouch.—The anal opening is situated in a well-defined pouch of somewhat crescentic shape, which measures 2 inches in breadth and about the same in depth.

The anal mucous membrane has a hæmorrhoidal appearance, though this is not so striking as figured by Murie in *H. brunnea.*

There are three large glands on each side of the rectum, dorsal, lateral or middle and ventral or anterior. In this respect *H. striata* differs from *H. brunnea*, which possesses only one gland on each side, and from *H. crocuta*, in which there is one on each side, and a belt of glandular nodules across the deep part of the pouch. It also differs, though not greatly, from the description given by Daubenton[1] of the arrangement in *H. striata.* Daubenton states that there are only two glands on each side, and he terms them anterior and posterior; but he says that, in addition, the upper wall of the anal pouch, between the rectum and the sacrum, is scattered over with glandular nodules, and he figures these as being most numerous on each side. This corresponds very closely with what obtains in our specimen, in which the two dorsal glands are united across the middle line by scattered glandular nodules. The single gland on each side in *H. crocuta* contains a large cavity opening by one duct into the anal pouch; it therefore corresponds with the

[1] *Loc. cit.*

gland we have termed lateral in *H. striata*, and with that which Daubenton calls anterior, the structural arrangements being the same. The belt of glandular nodules across the deep part of the pouch in *H. crocuta*, and that described as dorsal by Daubenton, agree in position with the dorsal glands and the connecting bridge of nodules in *H. striata;* the ducts from all the nodules open directly into the anal sac. The glands which we call anterior, and Daubenton speaks of as posterior, are evidently the same, the difference of nomenclature being due to the fact that we have described their position in the body, whilst Daubenton has described them as the separated organs lay on the dissecting table. The ducts of the nodules forming these glands open separately into the anal pouch.

Collectively, the anal glands of *H. striata* are larger than those of *H. crocuta;* together with the anal pouch they are enclosed by a strong sphincter muscle, some of the fibres of which pass between the individual glands.

Note.—In the next number of the *Journal* we hope to complete the paper by a description of the muscles and their nerve supply.

(*To be continued.*)

THE RECTUM AND ANUS. By J. SYMINGTON, M.D., F.R.S.E., *Lecturer on Anatomy, School of Medicine, Edinburgh.*[1]

MR FREDERICK TREVES, in his Hunterian Lectures in 1885 on "The Anatomy of the Intestinal Canal and Peritoneum," gave the following summary of the generally accepted view as to the position and direction of the rectum:—

"The rectum is divided into three parts. The first part commences at the sacro-iliac synchondrosis, and passes obliquely from left to right, forming a gentle curve to the right, and ultimately gaining the middle line opposite the third piece of the sacrum; it is entirely invested by a fold of peritoneum, called the meso-rectum. The second part extends along the concavity of the sacrum as far as the coccyx, at which point the third part begins, and inclines at once backwards to terminate at the anus."

Mr Treves showed that the sigmoid flexure and the first part of the rectum form a single loop, which cannot be divided into parts. This loop generally lies in the pelvis, but when distended it rises up, reaching, in some cases, as high as the under surface of the liver. He maintained that the usual description of the sigmoid flexure as lying, in the form of the letters S or Z, in the left iliac fossa, was altogether incorrect.

With reference to the remaining portions of the rectum, he expressed himself as follows, p. 60:—

"The descriptions given of the second and third parts of the rectum (the portions beyond the point of ending of the meso-rectum) I would fully endorse, both as regards the direction and position of the gut and its relations to the serous membrane."

My own observations support the views of Mr Treves as to the sigmoid flexure and the first part of the rectum; but I think there will be little difficulty in showing that his confidence in the accuracy of the usual account of the second and third parts of the rectum is misplaced. These portions of the bowel lie so deeply, and are surrounded so extensively by soft structures, that any attempt to investigate their topography by the ordinary

[1] Read before the Anatomical Society of Great Britain and Ireland, June 1888.

methods of dissecting is very liable to lead to erroneous conclusions.

In this paper I propose to give the results of the examination of frozen sections of a number of pelves. The sections were made in various planes, but those that afforded the most satisfactory results were cut in a transverse vertical or coronal direction.

Second Part of the Rectum.—The usual description of this part contains an important error, since it represents the bend which marks the junction of the second and third portions as occurring opposite the tip of the coccyx. Some authors omit any reference to the coccyx, but state that the second part ends at the prostate gland. In one text-book, viz., Wilson's *Anatomist's Vade-Mecum,* 10th ed., p. 697, the third part is said to curve backwards "from opposite the prostate gland and tip of the coccyx to terminate in the anus." It is evident that these two points are intended to indicate the positions where the anterior and posterior walls respectively turn downwards and backwards. Now, any good mesial section of the pelvis will show that the posterior-inferior wall of the second part of the rectum does not change its direction at the tip of the coccyx, but continues to pass downwards and forwards for an inch or more, lying beyond the coccyx upon a segment of the pelvic floor, which may be called the *ano-coccygeal body.* The term *perineal body* has been pretty generally adopted for the mass of tissue which, in the female, lies between the lower parts of the rectum and vagina. In both sexes there is an equally well-defined body lying between the tip of the coccyx and the anus. It is composed, like the perineal body, of muscular and fibrous tissue, and it forms an equally important constituent of the pelvic floor. When examined in a mesial or a coronal section it is seen to have a quadrilateral form. In any ordinary adult it is a little over an inch in length, about an inch from above downwards, and nearly the same from side to side. It is bounded behind by the coccyx and in front by the anal canal, the rectum rests upon its upper aspect, and its lower surface is formed by the skin. Its lateral boundaries are the fat of the ischio-rectal fossæ. It is formed mainly by the levatores ani and the internal and external sphincters. The arrangement of its

muscles is best demonstrated by a series of transverse sections passing from above downwards and backwards. Such a series of sections shows that the muscular fibres are best marked near the anus, becoming smaller in amount and being replaced by fibrous tissue towards the coccyx.

The anterior and upper wall of the second part of the rectum, after leaving the bladder, lies in close contact with the posterior surface of the prostate. At the apex of this gland it begins to bend downwards and backwards, so as to become continuous with what is generally called the third part of the rectum. This bend in the anterior rectal wall sometimes forms a distinct *cul-de-sac*, which lies below the prostate and points towards the membranous part of the urethra and the bulb. This pouch may become, as Kohlrausch showed, very well developed, as the result of distension of the rectum. I have a specimen, however, in which it is distinct, although the rectum is quite empty.

W. J. Otis[1] has proved that the rectum is not an even cylindrical tube, but is sacculated, the so-called valves or folds of the rectum being the constrictions between the sacculi. Many anatomists describe a special dilatation of the rectum situated immediately above the anus, and known as the ampulla. It is supposed to be the largest part of the rectum, and to serve as a reservoir for the fæces. I have a series of horizontal sections through the pelvis of a man aged 57 years, in whom the whole length of the rectum was packed with fæces. About 2½ inches above the anus the diameters of the rectum were 7 cm. from side to side, and 4 cm. from before backwards. The portion of the rectum below this gradually diminished in size, resembling in shape a cone, the blunted apex being directed downwards and forwards to the upper opening of the anal canal.

Third Part of the Rectum and the Anus.—The former is generally described as passing downwards and backwards for about an inch and a half, and then to end in the latter. In entering upon an examination of this statement, it will be necessary to consider what constitutes the anus, as distinguished from the rectum. Those who describe a third part of the rectum running downwards and backwards for an inch and a half evi-

[1] *Anatomical Researches in the Human Rectum*, part i., "The Sacculi of the Rectum," Leipzig, 1887.

dently mean by the anus the aperture situated opposite the junction of the skin and mucous membrane. In fact, a mere orifice or ring, and not a passage of any appreciable length. I believe this view to convey an erroneous conception of the normal condition of the parts, and to lead to incorrect ideas as to the physics of the pelvic floor and the mechanism of defæcation. The rectum is a receptacle for fæces or air, and these may be retained in it for a longer or shorter time; while the anus is a passage, between the rectum and the exterior, which is surrounded by certain sphincters, and has its walls in close contact except during defæcation. This passage, the anus or anal canal, is about an inch in length, and its long axis is directed downwards and backwards at about a right angle with that of the second part of the rectum. It includes what is frequently described as the third part of the rectum and the anus.

My attention was first specially directed to the condition of the anus by a series of interesting articles on "The Topographical Relations of the Female Pelvic Organs," by Professor Ranney, which appeared in the *American Journal of Obstetrics* for 1883. Ranney was not disposed to place much reliance upon the results of frozen sections in determining the topographical anatomy of the female pelvic organs; and he advanced as a proof of their unreliability the fact that nearly all the published plates representing mesial sections of the frozen pelvis depict the anus as an open tube. He says (p. 238) that

> "The open anus so commonly depicted in most of the gynæcological contributions is inaccurate, if the condition which exists during life is to be properly represented. This condition may exist in frozen sections, but never during life, as any careful observer can attest, provided the sphincters of the rectum and the levatores ani muscles are performing their proper function."

Mesial sections undoubtedly show the anterior and posterior boundaries of the anus separated by a distance of from half an inch to one inch. Any one who has had experience in preparing frozen sections of the pelvis knows the difficulty of getting a good section through the anus; in fact, after an attempt has been made to do so with a saw, it is generally necessary to take a slice of one or other of the lateral slabs in order to completely open it. This difficulty is due to the fact that the anal canal is

an antero-posterior slit, its lateral walls being in close contact with one another. In most of the representations of mesial sections of the pelvis, the anal canal is shaded rather too deeply, for if fresh sections be examined, the lateral wall of the anal canal will be found to be close to the surface of the section.

Ranney gave a schematic drawing of a sagittal section of the female pelvis and its organs,[1] which he considered to represent, more accurately than a drawing of any frozen section, the natural relations of the parts.

Fig. 1 is after Foster, modified by Hart and Barbour, but it

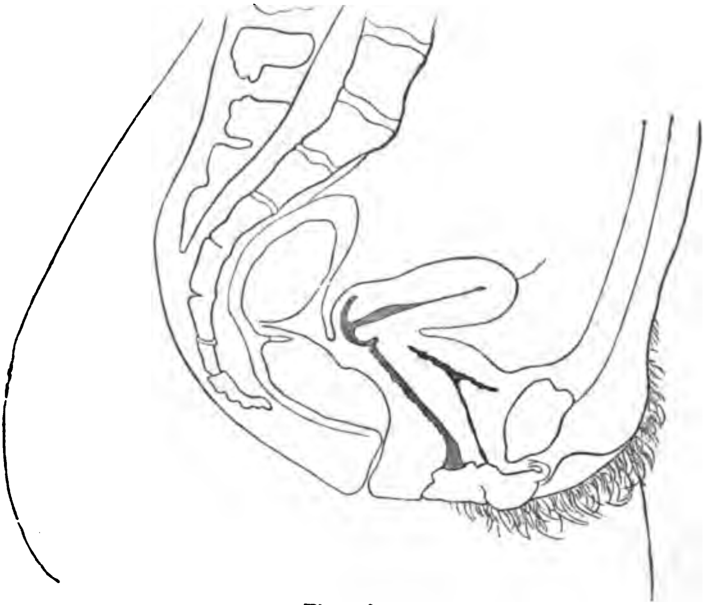

Fig. 1.[2]

shows the relations of the rectum, anus, and ano-coccygeal body in a manner practically identical with Ranney's own diagram.

Ranney represents the anal canal with its anterior and posterior boundaries close to one another, while the rectum, when empty, has its lateral walls in contact. In Ranney's own drawing the length of the ano-coccygeal body is fully three times greater than its thickness. His opinion that the lower

[1] *Amer. Jour. of Obstet.*, vol. xvi. p. 370, fig. 11.

[2] I have to thank Dr Berry Hart for the use of electros of figs. 1, 2, 4.

part of the rectum collapses by the opposition of its lateral walls is based upon a drawing (see fig. 2) in Henle's *Handbuch der Anatomie*, Bd. 3, p. 462. Henle gives no particulars as to how the specimen was prepared, but he describes it as a horizontal section of the soft parts at the pelvic outlet, including the urethra, vagina, and rectum. All these passages are represented as closed, the urethra appearing as a transverse slit, and the vagina as a transverse slit with a longitudinal one at each extremity. The other passage, I believe, represents a section

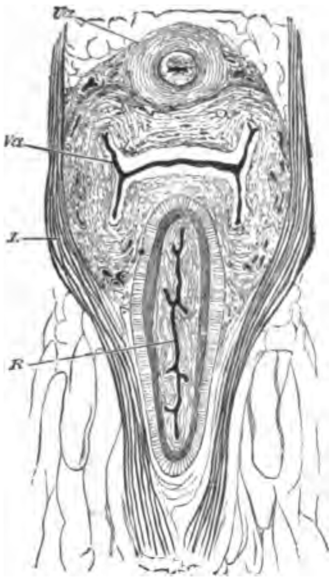

Fig. 2.

through the anal canal instead of the rectum. The peculiar shape of the vaginal canal indicates that it was divided towards its lower end, and a section going through it and the urethra, if continued backwards, would cut across the anal canal.

My own observations support the view of Dr Berry Hart[1] that the lower part of the empty rectum has its anterior and posterior walls in contact. This is what I have found in frozen sections, and a consideration of the direction of intra-abdo-

[1] "On some Points in the Physics of the Bladder and Rectum," *Edin. Med. Jour.*, 1882.

minal pressure renders it extremely probable that such will also be the case during life.

The relations of the pelvic viscera have been chiefly studied by means of vertical mesial sections, but good sections of the anal canal in this direction are difficult to prepare, and when made do not show satisfactorily its relations to the external sphincters and levatores ani. On the other hand, the anal canal can readily be opened by transverse sections made in a direction from above downwards and slightly backwards, and specimens prepared in this way demonstrate some important points with regard to its relations to muscles.

Fig. 3 shows a section of this kind looked at from behind, from a female subject, aged 54 years. The entire body was

FIG. 3.—*v*, Vagina ; *r*, end of 2nd part of rectum ; *i.s.*, internal sphincter ; *e.s.*, external sphincter ; *l.a.*, levator ani. The interval between the levator ani and external sphincter was less than that represented in this woodcut.

frozen. The section through the bony pelvis was a little posterior to the anterior extremities of the iliac crests, and passed downwards, just behind the hip-joints, to the ischial tuberosities. The pelvic viscera divided were the bladder, vagina, rectum, and anal canal. The bladder contained about 20 ounces of urine. The vagina was in the form of a transverse

slit, about 1¼ inch long. The rectum was divided close to its anterior extremity. It contained a small quantity of fæces. The anal canal was opened in its entire length. Its lateral walls were in close contact. On separating them the mucous membrane was seen to be thrown into numerous longitudinal folds (the columns of Morgagni), but the canal was essentially a longitudinal slit. Below the anus the skin of the opposite buttocks was not in contact. In a corresponding section in a male subject, aged about 20, the anal canal presented a very similar appearance to that of this female, but below the anus the skin of the buttocks was in close contact for more than an inch. In the male subject the rectum was empty, and the cavity of the rectum immediately above the anal canal presented the form of a distinct transverse slit. The inclination of the anal canal from above downwards and slightly backwards facilitates the expulsion of fæces through it, since intra-abdominal pressure can act most favourably upon the pelvic contents in that direction. This arrangement, however, must, to a certain extent, be a source of weakness to the pelvic floor, since it facilitates the forcible opening of the anal canal during the contraction of the diaphragm and the muscles of the abdominal walls. This source of weakness will be found to be guarded against by the special provisions that exist for the closure of the anal canal, and I believe that these will be found to be more powerful than is generally supposed.

It has already been stated that the anal canal exists in the form of a longitudinal slit, with comparatively small folds on its lateral walls. It is interesting to note that almost all the canals that are normally closed, such as the vagina, urethra, and Eustachian tube, have this slit-like form, and are not reduced to a minute ring or a stellate opening. It is probable that these slit-like openings can be closed with the least expenditure of muscular force.

Of the muscles lying in relation to the anal canal the two sphincters call for but little notice. The internal sphincters surround the whole length of the anal canal except close to its lower end. If the fibres of the external sphincter be divided transversely at the anus they will be found to form on each side a curved mass, which lies partly below the internal sphincter,

and corresponds to the junction of the skin and mucous membrane, and partly on the outer side of the lower part of the internal sphincter, and internal to the fat of the ischio-rectal fossa. While there is but little difference of opinion as to the arrangement and action of these two sphincters, it is quite otherwise with regard to the levatores ani, anatomists being by no means agreed as to either the course or the action of their fibres. The ordinary name of "levator ani," as well as that of "musculus sedem attollens" given to it by Vesalius, represents an ancient and a pretty generally accepted view that it acts as an elevator of the anus. Some of its fibres are frequently described as passing downwards and inwards to the anus, where

Fig. 4.

they blend with the external sphincter, and also to a slight extent with the internal sphincter. These fibres have been regarded as dilators of the ani, and thus antagonistic to the sphincters.

Cruveilhier,[1] in opposition to this view, asserted that the direction of its fibres is such that it must act along with the sphincters as a constrictor of the anus. On the other hand, Luschka[2] maintained that only a few of its fibres are able to assist the sphincters. The drawing (see fig. 4), however, which he gave of the muscle represented the anterior fibres as running backwards from the pubes towards the coccyx, and crossing the bowel a little above the external sphincter.

[1] *Traité de Anatomie*, 5th ed., tome ii. p. 446.
[2] *Anatomie des Menschen*, Bd. 2, p. 148.

I am indebted to Mr Lockwood for directing my attention to some observations on these muscles which he made with Mr Harrison Cripps, and which are recorded in a work by the latter entitled *Diseases of the Rectum and Anus*, London, 1884.

They describe a large portion of the fibres of the levator ani as arising from the inner surface of the symphysis and about half an inch of the anterior portion of the white line, and as passing downwards and backwards to be inserted on the sides of the coccyx. When these fibres contract simultaneously with those of the opposite side "they will act powerfully as compressors of the rectum, squeezing the sides of the canal together as it passes between their two inner surfaces." Mr Cripps believes that the contraction of these portions of the levatores ani can be felt on digital examination of the rectum in the living body.

These observations agree to a certain extent with my own, especially in so far as they show that a number of the fibres of these muscles pass from and near the pubes backwards round the sides of the bowel towards the coccyx. I consider, however, that these fibres assist the sphincters in closing the anal canal, but do not compress the bowel beyond the level of the internal sphincter.

The position and relations of the levatores ani are well seen in a series of coronal sections of the pelvis. In the preparation represented in fig. 3, the fibres of the levatores ani formed a well-defined mass external to the anal canal and internal sphincter, and above the external sphincter. The fibres situated above and external to the anal canal were much fewer than those at its sides. All the fibres were cut across at more or less of a right angle to their direction.

The actions of the levatores ani in connection with defæcation appear to me to be as follows:—When the fæces have been forced by vermicular contraction into the lower part of the rectum, they can assist the sphincters in preventing the passage of the fæces through the anal canal. During defæcation they will be relaxed along with the sphincters, the anal canal is opened, and the ano-coccygeal body pushed downwards and backwards. Towards the end of the act of defæcation the levatores come into action in closing the anal canal and drawing the ano-coccygeal body upwards and forwards.

ON THE GROWTH-RATE OF THE BONES OF THE LOWER EXTREMITIES, WITH ESPECIAL REFERENCE TO RICKETTY CURVATURES.[1] By WALTER PYE, F.R.C.S.

THE points which I wish to bring before the consideration of the Anatomical Society to-day are the outcome of observations and measurements made chiefly at the Children's Hospital during the past five years, with the following objects:—

1. To ascertain the average growth-rates of the thigh and leg bones during childhood, taking childhood to run from the second to the eighth year inclusive.
2. To contrast these rates with those obtained by measurement of limbs which are the subjects of ricketty curvatures.
3. To estimate the effect of these curvatures upon the apparent stature of such children, and upon their apparent and real growth during and after the development of the curves.
4. To estimate in these cases the value of the growth of the bones of the thigh and leg as making for recovery of the natural straightness of the limb.

Methods of Investigation.—We all know that even in an adult, and when the bony prominent landmarks are definite and easy to find, it is yet a matter of common occurrence for two reasonably intelligent and careful people to differ to the extent of $\frac{1}{4}$ or $\frac{1}{3}$ of an inch, or even more, when measuring, without any bias, conscious or unconscious, being present one way or another, say the length of the lower limb. It will, therefore, readily be understood that in the case of children, often plump, always restless, and with bony prominences very indefinite and difficult to localise, the task of measuring month by month, legs or thighs, in which the normal increase of growth will generally be less than $\frac{1}{8}$ inch, would be one from which it would be hopeless to expect any trustworthy results if the measurements were made in the ordinary way from bony point to bony point. But, on the other hand, it may, I think, be allowed that if the periodic measurements are made with the limbs always in the

[1] Read before the Anatomical Society of Great Britain and Ireland, April 1888.

same position, and are always taken between exactly the same points, marked on the skin, only roughly corresponding with the bony prominences ordinarily taken, then the increase of distance between such points may be reckoned as equivalent to the increase in length of the bones beneath. The plan I have adopted, therefore, has been, in all cases where it was desired to establish the growth of the thigh or leg, to place the child upon a board or table, such as the one produced, which is as you see ruled into rectangular squares of 2 inches, and which has for convenience a rough inch measure all along its sides.

As all the lines on the board are parallel or at right angles to each other, it is as a rule easy to be certain, when the child is placed upon it, that it lies fair and square each time it is measured, but if it should not do so for any reason, then, in order to secure that the condition remain the same, all that is necessary is to place between the legs and the board a sheet of paper similarly ruled in 2-inch squares, make these correspond with the board squares, and with a pencil held at right angles roughly trace the outline of the limbs as they lie upon the paper.

I have here some of such tracings, but it is not often necessary to take them for the mere purpose of accurate measurement; they do, however, form fairly accurate records of progress in the case of tibial and femoral curvatures. Further, these tracings can be easily reduced, as the accompanying diagrams will show.

Similar position thus secured, the other requirement, measurement from identical points, I have managed by making a very fine tattoo point over the anterior iliac spine, one over the interval between the outer tuberosity and the head of the tibia, and one over the lower border of the external malleolus. This tattooing is done with a very sharp grooved point (the last $\frac{1}{8}$ of an inch of a common grooved needle in fact), set in a handle, and which I here show. It is charged with Indian ink. The skin being sharply pricked once at the point selected, no pain is given, and a very fine permanent dot remains—permanent, that is, sufficiently for our purpose, for it can always be renewed if necessary, and will otherwise begin to fade in about nine months or a year's time.

Between fine points such as these it is not difficult to measure even to $\frac{1}{32}$ of an inch, and to $\frac{1}{16}$ of an inch it is easy to

be accurate, provided that a precaution which I believe to be essential be taken, namely, to measure with a plain tape or rule: one that is without any division marked upon it.

But before we deal with the especial question of the growth-

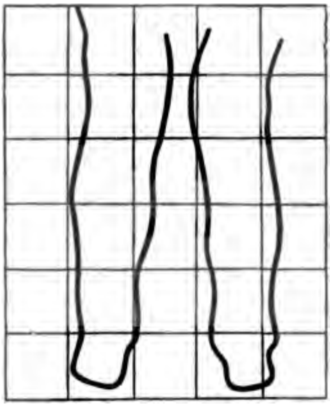

FIG. 1.—P. R., Jan. 11, 1888.

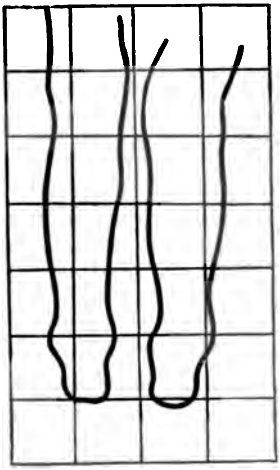

FIG. 2.—P. R., March 21, 1888.

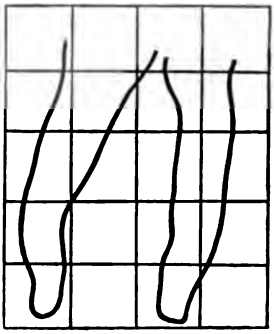

FIG. 3.—G. H., Jan. 17, 1888.

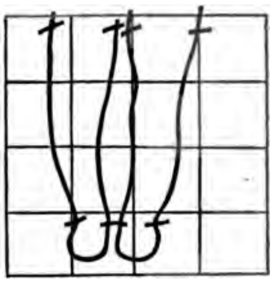

Fig. 4.—G. H., April 15, 1888.

FIGS. 1–2 and 3–4 are examples of tracings from the tracing board, described in the text and reduced for reference, each square = 2 inches.

rate of the lower extremities, it will be necessary to trouble you with certain tables and data as to the growth-rate of the whole body between the ages I have mentioned.

From the 1883 Report of the Anthropometric Committee of the British Medical Association, it appears that the height and growth-rate of children brought up under the most unfavourable

conditions, *i.e.*, industrial school children, may be estimated as under:—

TABLE I.—*Height and Growth-Rate of Industrial School Children.*

No. of Observations.	Age.	Sex.	Height.		Increase.
			feet.	inches.	inches.
11	2	M.	0	·0	...
		F.	2	7·95	...
15	3	M.	2	10·50	...
		F.	2	11·50	3·4
28	4	M	3	0·27	1·8
		F.	3	1·07	1·5
30	5	M.	3	2·63	2·4
		F.	3	3·22	2·2
92	6	M.	3	5·14	2·5
		F.	3	5·15	1·9
109	7	M.	3	7·54	2·4
		F.	3	6·38	1·2
135	8	M.	3	8·61	1·1
		F.	3	8·68	2·3

From the same source I obtain the following table:—

TABLE II.—*Average Height and Growth-Rate of Children of all Classes.*

Age.	Sex.	Height.		Increase.
		feet.	inches.	inches.
2	M.	2	9·7	...
	F.	2	8·3	...
3	M.	3	0·8	3·1
	F.	3	0·0	3·7
4	M.	3	2·4	1·6
	F.	3	2·1	2·1
5	M.	3	5·0	2·6
	F.	3	4·8	2·7
6	M.	3	8·0	3·0
	F.	3	6·6	1·8
7	M.	3	9·9	1·9
	F.	3	8·4	1·8
8	M.	3	11·0	1·1
	F.	3	10·6	2·2

I have compiled a similar table of the average height and rate of growth of what may be termed the most favoured classes, the "upper middles," as our slang phrase has it, from too small a number of cases to be altogether authoritative, still it will probably be sufficiently correct.

TABLE III.—*Height (and Growth-Rate) of 62 Children of the most Favoured Classes.*

No. of Observations.	Age.	Height.		Increase.
		feet.	inches.	inches.
8	2	2	10·6	...
9	3	3	2·3	4·7
7	4	3	4·8	2·5
12	5	3	6·9	2·1
14	6	3	8·2	1·3
6	7	3	11·3	3·1
6	8	4	1·5	2·2

In this table it has not seemed worth while to separate the sexes, but it will be seen that the rate is considerably higher than in either of the former ones.

We shall now be able by comparison to ascertain if the general growth-rate of the hospital patients, the particular rate of whose lower extremities I have been wishful to determine, is below, up to, or above the average. With regard to this point, I had expected to find that the figures would work out something as do those of the measurements in Table I. (industrial schools), but I find that the heights of 54 children attending hospital, whose local ailments were not of a nature to affect their stature or growth, come out, when tabulated, somewhat above the average, as given in Table II.

TABLE IV.—*Heights of 54 Children, Hospital Patient Class, without any Ailment diminishing Stature.*

No. of Observations.	Age.	Height.	
		feet.	inches.
6	2	2	10·0
9	3	3	1·8
10	4	3	3·9
7	5	3	5·8
7	6	3	7·0
9	7	3	10·2
6	8	3	11·4

We may assume, then, that the class of children whose lower extremities were measured in the way I have above described were specimens of fair average development and growth. Of

such the following general statements of growth may be accepted:—

That the most rapid increase in height takes place during the first five years, and is about the same in boys and girls, and that for the next four years or so boys grow somewhat faster than girls.

The period of greatest increase is in the first year, when it averages 7¾ inches, next in the 2nd, about 4 inches, and thenceforward gradually declines to about 1¾ inches at the twelfth year (with frequent exceptions).

Now, with regard to the proportion of these increments which should be assigned to the growth of the lower extremities, it is stated that during the whole period of growth the lower extremities become five times their original length, while in the same time the head and neck only doubles its length, and the trunk only trebles it.

But it is in the early years of life that by far the greatest thigh and leg growth occur; so much so, that by the end of the third year the lower extremities have already doubled their original length (the thigh now, as always, having grown a little more than the leg). The twelfth year is reached before they quadruple it, and the remaining years are required to complete the quintuple growth. It is obvious, therefore, that upon the growth of the legs and thighs *in early life* depends in an especial fashion the future stature of the individual, and that particularly during the years in which it is believed that children are specially subject to diseases arresting or retarding development.

It is then, I think, a matter of practical importance to determine, if possible, the average growth-rate for these earlier years of the thigh and leg by measurements taken at much shorter intervals than once a year.

I have found, however, that even during the second year monthly intervals are too short for trustworthy measurements, and that at intervals of two months they are much easier to take, to say nothing of the labour involved by the former plan. A further series of eighteen children in their second year of age gave practically the same result when measured at two months' intervals. Eighteen children were measured at two months'

intervals during their third year, and thirty-four at three months' intervals from the fourth to the eighth year, with results which I may summarise thus:—

Turning to the second year, the thighs grow at first at a rate of a little more than $\frac{1}{7}$ inch, and the legs a little less than $\frac{1}{7}$ inch a month; this gradually diminishes, until at the end of the year the rates are $\frac{1}{10}$ and a little more than $\frac{1}{12}$ respectively. During the third year the monthly growth-rate is a little more, and a little less for thigh and leg than $\frac{1}{12}$ inch, and so on, in diminishing rates, until the eighth year, when the monthly ratio have sunk to $\frac{1}{18}$ and $\frac{1}{20}$ inch. I should add that one limb only of each child was used for measurement.

TABLE V. *shows the Average Growth of the Thighs and Legs in* 14 *Children measured at Monthly Intervals during their Second Year.*

Age.	Increase since Last Measurement.			
Months.				
13	Thigh,	·15 inch.	Leg,	·14 inch.
14	,,	·14 ,,	,,	·12 ,,
15	,,	·13 ,,	,,	·11 ,,
16	,,	·13 ,,	,,	·12 ,,
17	,,	·12 ,,	,,	·10 ,,
18	,,	·10 ,,	,,	·09 ,,
19	,,	·12 ,,	,,	·09 ,,
20	,,	·12 ,,	,,	·10 ,,
21	,,	·10 ,,	,,	·08 ,,
22	,,	·10 ,,	,,	·08 ,,
23	,,	·10 ,,	,,	·09 ,,
24	,,	·10 ,,	,,	·08 ,,
Total increase, . .		1·40 inch.		1·20 inch.

It remains for us to see how these results compare with similar measurements taken on children who were the subjects of ricketty curvatures, in the course of development, when they were first seen.

Of these cases it is commonly said that during the attack the growth of the limbs and trunk is retarded or arrested; and, inasmuch as it is especially in the second and third years that rickets is apt to appear, if the very rapid growth at these ages is kept in mind, it will become obvious that any marked arrest of

development is then much more important than it would be later on in the child's life.

No doubt, in the severe and marasmic cases of the disease the whole growth of the body is retarded, as it is in any other acute disorder of nutrition. But it will be within the experience of all that many ricketty, bandy-legged, or knock-kneed children have a very fair condition of general health, the while that their legs are bending under the weight of their heavy lumpy bodies.

In such cases it will, I believe, be very commonly found that, while the ricketty yielding of their legs persists, they may seem hardly to grow in stature, and even (as in some cases I have known) apparently to be shorter at the end of six months than they were at the commencement. Nevertheless, if we watch the growth of these patients for a further term of a year or two, we shall find that they are not being permanently dwarfed or stunted, and that they will eventually evidence few if any signs of the deformities which were at first so conspicuous.

A great agent, perhaps the chief one, in this readjustment of stature, is, I believe, the fact that, during the period of development of the femoral and tibial curvatures, the growth-rate of the bones is not as a rule diminished (cases of acute rickets with marasmus being excepted). I have measured altogether sixty-seven children, of ages between 18 months and 4 years, who were the subjects of well-marked femoral and (especially) of tibial curvatures, and I have found that the actual growth of the leg and thigh is not, on the average, less than the growth of a straight limb at the same age; provided, of course, that the real length of the limb, not the length of a straight line from point to point, be taken.

If this be the case, I would (although this is rather a surgical than an anatomical question) submit that when we see, as we do see every day, children who have become bandy-legged, quickly recovering from their deformities as soon as their legs are relieved from the weight of their bodies, whether it be by splints or in any other way, we should recognise that this is due rather to the very rapid growth of the lower extremities at this age than to any moulding or coercive power which mechanical appliances can exercise.

ON SOME POINTS IN THE ANATOMY OF A *MEGAPTERA LONGIMANA*. By JOHN STRUTHERS, M.D., *Professor of Anatomy in the University of Aberdeen*. (PLATE VI.)

(Continued from vol. xxii. page 654.)

PART III.—*continued*.

CERVICAL VERTEBRÆ.

The measurements in the following Table may be compared with those given in the Table of Measurements of three series of the cervical vertebræ of B. musculus, in this *Journal*, vol. vii., November 1872.[1]

[1] The paper referred to, "On the Cervical Vertebræ and their Articulations in Fin-Whales," contains a full account of the characters of the cervical vertebræ in Balænoptera musculus and in B. rostrata, and of their articular surfaces and ligaments, including the variations presented by the three complete sets of the cervical vertebræ of B. musculus and by other specimens of atlas and axis of that species. The characters in B. musculus there described are assumed here, and are occasionally referred to only for comparison with those of Megaptera. It will be understood that "the B. musculus" noted in the following account is the 50-feet-long B. musculus with which the Megaptera is compared throughout this paper, unless the other specimens described in the previous papers are mentioned.

30. TABLE V.—*Measurements of the Transverse Processes of the Cervical Vertebræ, in addition to those contained in Tables II. and III., given in inches.*

	Megaptera.							B. musculus, 50 feet long.						
	Atlas.	Axis.	3	4	5	6	7	Atlas.	Axis.	3	4	5	6	7
1. Length of upper, . .	3¾	6½	6	6¼	6½	6½	6	6½	10¾	9½	9	9	8½	8½
2. Length of lower, . .	...	5½	3½	2¾	½	...	...	...	10	7½	7½	8½	3½	...
3. Breadth of plate beyond the rings.	...	...	...	...	...	...	...	...	5	...	...	...	...	..
4. Transverse diameter of the rings.	...	...	...	...	...	...	...	...	5½	7	7	6¾	...	...
5. Greatest distance between upper and lower processes.	...	3⅝	5½	6	...	...	...	...	3½	6	6½	6⅛	6¾	...
6. Distance between their ends.	...	3	5⅝	6	...	...	...	...	...	1½	1½	½	5½	...
7. Weight in ounces,[1] .	209	176	...	54	...	...	73	176	212	...	79	...	...	108

31. THE ATLAS—*Anterior Aspect.*—The groove between the condyloid cavities is wide. This might seem to be a distinctive character in contrast with the narrowness of the groove in B. musculus, as seen in four of my specimens. In two of them it is reduced to the condition of a mere median furrow. But in the 50-feet-long B. musculus the width is not much less than in the Megaptera. In the latter the width is—below, which is also the narrowest part, 1½ inch; at middle, 1¾; above, 2⅝. In the B. musculus, the corresponding measurements are, 1½, 1½, and 2⅛ inches; the narrowest part, towards the lower end, 1¼. The widest in the other four specimens of B. musculus is ⅝ inch, and the groove has that width nearly all along. In both the Megaptera and the 50-feet-long B. musculus the furrow for the capsular ligament of each condyle is seen at the edge of the wide groove. In the dissection (1872, *loc. cit.*, p. 14) I found the median interval so narrow that the two capsular ligaments seemed to have coalesced, and the median septum thus formed to be disappearing, but I could not be quite sure that the seeming partial disappearance of the median septum was not due to giving way of the parts. The narrowing of the space

[1] The weight of the first caudal vertebra is, in Megaptera, 304 ounces, in the B. musculus, 368 ounces.

between the condyloid cups, as seen in these five specimens of B. musculus, may be a matter of age, but in the atlas of a sixth great finner (referred to, *loc. cit.*, 1872, p. 15 and p. 45), larger than any of the other five, the median groove is broad; at the narrowest, at an inch from the lower end, $1\frac{1}{8}$ inch, at the middle $1\frac{3}{4}$, near the canal $1\frac{7}{8}$. It may possibly become narrower with age in Megaptera also.

The inferior ends of the condyloid cups project more than in B. musculus. This projection in the forward direction renders the cup somewhat deeper than in B. musculus; but the chief difference is the greater downward projection, by which in Megaptera the cups project below the level of the inferior arch of the bone, leaving a wide and deep notch between them. In the four mature specimens of B. musculus the rough anterior arch is seen below the level of the cups, and the notch between the slightly raised inferior ends of the cups is shallow, $\frac{1}{4}$ to $\frac{3}{4}$ inch deep, and about 3 inches wide, but in the largest atlas (the Wick specimen) considerably narrower. In the Megaptera the notch is $1\frac{1}{2}$ inch deep, and, in width, $3\frac{1}{2}$ inches below, $1\frac{1}{4}$ above. In the 50-feet-long B. musculus the distinction is much less marked, the notch 1 inch deep and wider below than in Megaptera, and the cup projects below the level of the inferior arch of the bone. But allowing for the immaturity of both, as compared with the four first-mentioned specimens of B. musculus, it appears that the lower ends of the cups project considerably more in Megaptera than in B. musculus, giving both a deeper cavity and a greater projection downwards.

Posterior Aspect of the Atlas.—The chief characters on this aspect of the atlas are (*a*) the presence of a mesial articular surface, dividing into three parts what forms one great horseshoe articular surface in other finners, and (*b*) the form of the ligamentous area.

(*a*) *Mesial Articular Surface.*—The position and characters of this surface are seen in fig. 17. It occupies the whole height and breadth of the inferior arch of the bone; in form resembling the upper half of a blunt oval, height $2\frac{1}{2}$ inches, width 3 inches, vertically convex on its upper half, on its lower half a little concave. It is bounded below by the triangular

subaxial peak, here ½ inch in length, which meets it at nearly a right angle. This aspect of the subaxial peak has somewhat the appearance of having on it an articular facet the size of the end of a finger, but there is no corresponding facet on the axis.

The mesial articular surface is separated from the great semilunar lateral surface by a furrow ¼ to ⅜ inch in breadth; in length 1½ inch on the right side, ¾ inch on the left. Although the separation of the mesial surface is very marked on the macerated bone, it does not follow that it was separated by ligament, or even that the articular cartilage was not continuous with that on the lateral surfaces. The floor of the furrow is not rough, and the levels of the surfaces on either side are nearly the same, the surface on the outer side of the furrow a little more projecting.[1]

(*b*) *The ligamentous area*, for the attachment of the great interosseous ligament on each side between the atlas and axis, crescentic in form in all the specimens of B. musculus, is quadrate or rhomboidal in Megaptera; also much broader, and altogether considerably larger than in B. musculus (see fig. 17, and, for comparison, fig. 5, Plate II., *loc. cit.*, 1872, showing the form in B. musculus, and also the transverse ligament). In Megaptera the length of the area averages 3½ inches, breadth about 2¼, at its lower part 2 inches. The greater breadth and quadrate form in Megaptera are gained above by its throwing out a superior external angle, prolonged like the point of a finger; below, by its extending as an inferior external angle between the mesial and lateral articular surfaces; and internally by the boundary of the canal being less curved outwards than in B.

[1] Professor Flower has described (*Proc. Zool. Soc.*, 1864, p. 402), on the atlas of the fin-whale in the Leyden Museum, taken on the north-west coast of Java, the lateral articular surfaces as not confluent below, but having between them "a distinct, oval, transversely elongated facet, and another smaller round one is situated on the upper surface of a pointed triangular projection from the hinder border of the inferior surface of the bone, which runs under the body of the axis." Also corresponding surfaces on the axis. The interval, shown in his figure (fig. 12) of the axis, between the median facet and the great lateral surface is considerable. In my B. borealis the two lateral surfaces are confluent, as in B. musculus, and there is no articular facet on the subaxial peak. In my figure of the posterior surface of the atlas of B. musculus (*loc. cit.*, 1872, fig. v.) a narrow median furrow is seen separating the great lateral articular surfaces, but reasons are given (*loc. cit.*, pp. 15 and 50) for not regarding that as implying non-continuity of the articular cartilage.

musculus. All round its upper, outer, and inferior margins the area is defined by the sharp edges of the articular surfaces. The sharp edge crosses the upper end of the furrow between the mesial and lateral articular surfaces, and the surface of the furrow resembles that of the articular surfaces, not that of the ligamentous area. The surface of the area is undulating and rough, excavated along the outer half, deeply pitted at the superior external angle, especially on the left side, less irregular but more rough along its inner half. Internally it is bounded by a sharp edge where it meets, at a right angle, the narrow surface bounding the canal. In the specimens of B. musculus this angle is rounded off.

The *great lateral articular surfaces* present less general convexity than in any of my five specimens of B. musculus. Internally the surface is encroached on by the ligamentous area, and on the outer half it is either nearly flat or a little concave transversely. In the specimens of B. musculus the surface has a marked transverse convexity, with a little concavity towards the outer part near the raised outer edge. Instead of the more or less raised articular surface, bounded by a sharp edge, seen in B. musculus, the upper half of the articular surface in Megaptera is, as it were, scooped out to the level of the concave posterior surface of the transverse process. The less convexity of the surface, together with the greater ligamentous area, in Megaptera would seem to indicate adaptation to less movement between the atlas and axis and more firm binding of these two vertebræ together in it than in B. musculus.

Canal of the Atlas.—The canal presents some differences from that of B. musculus. The height ($7\frac{1}{4}$ inches) is less than in any of the five specimens of B. musculus ($7\frac{3}{4}$ to 8 inches); in the 50-feet-long B. musculus almost 8. This is probably owing to the height of the inferior arch ($3\frac{5}{8}$ inches on the anterior aspect), which is about $\frac{3}{4}$ inch greater in Megaptera than in the 50-feet-long B. musculus. The lower end of the canal has thus a less pointed form than in B. musculus. The lower, or odontoid, part of the canal, marked off from the neural part by the constriction, varies a good deal in breadth in the different specimens of B. musculus. Especially in two of the specimens previously noted (*loc. cit.*, 1872) this part of the canal is much narrower

than in Megaptera, but in the 50-feet-long B. musculus it is the reverse; breadth at the narrowest part—in Megaptera 3 inches, in the B. musculus 3¼; at the widest part below—in Megaptera 3½, in the B. musculus 4⅛. Between these points is the place of attachment of the transverse ligament. It may be that the narrowing of this part of the canal depends on age.

Parts on the Neural Arch of the Atlas.—The *true articular processes* which I described (1872, *loc. cit.*, p. 39) in B. musculus are present in this 50-feet-long B. musculus, oval facets 1¾ inch transversely by 1¼ longitudinally; those of the atlas received obliquely between those of the axis, the typical relation of true zygomal processes. In Megaptera there is no trace of such articular contact, or of processes on the atlas, but distinct and large processes project here from the *axis* in the same position as the projections on which the articular facets occur in B. musculus. They are about 1¼ inch in length, and fully 3 inches broad at the base, narrower and rounded off at the end. When the bones are placed in position, these anterior articular processes of the axis overlap the lamina of the atlas for fully 1 inch, but there is no actual contact, a space of about ¼ inch intervening between them and the arch of the atlas.

Transverse Foramen of the Atlas.—In all the specimens of B. musculus the outer opening of this foramen or canal is oval vertically, the lower and outer end prolonged as a groove. In Megaptera the oval is nearly reversed, the ends anterior and posterior. This is owing to the roof of the canal being continued farther outwards in Megaptera. From the same cause the canal is longer by half an inch in Megaptera (1¾ inch) than in the 50-feet-long B. musculus. It is also rather smaller, in Megaptera admitting the forefinger, in B. musculus admitting the thumb. In all the specimens of B. musculus the bridge completing the canal is arched forwards, where it joins the posterior end of the condyloid cup, while in Megaptera the anterior margin of the lamina is almost straight from the end of the articular cup to the spine. The arching forwards is not owing to greater thickness of the bridge in B. musculus, the thickness being about the same (¾ inch) in Megaptera as in the 50-feet-long B. musculus.

Spinous Process of the Atlas.—There are marked differences

in the spine. In all the specimens of B. musculus, the spine, besides being low, is much more developed on the posterior half of the arch, in two of them very little developed on the anterior half. In Megaptera it is higher (1¼ inch, against about ¼ inch in the B. musculus), is semicircular in form, and rather better developed on the anterior than on the posterior half. In connection with this more anterior development of the spine is to be noted the straightness of the anterior border of the lamina in Megaptera, and also its thickness (⅜ to ⅝ inch), while in B. musculus it is a depressed sharp border.

Transverse Processes of the Atlas.—While the transverse processes of the specimens of B. musculus differ from each other in detail, those of Megaptera have characters distinct from them all. The difference is mainly in their shortness (in Megaptera 3¾ inches, in the 50-feet-long B. musculus 6¼). The farther out position of the internal intertransverse tubercle (external to the line of the outer edge of the condyloid cup, and at about the middle of the upper edge of the process) gives the process a more square shape in Megaptera, as seen antero-posteriorly. The process is also broader externally in Megaptera, but this is mainly owing to its wanting the outer half, which forms the tapering, bent-back, and twisted part of the process in B. musculus. The breadth (height) of the process at the middle, at the internal intertransverse tubercle, is 4½ inches, being greater than the length. Another character, also contributing to the square appearance of the process, is the abruptness of the junction of its lower border with the side of the body, compared with the gradual sloping-down of this junction in B. musculus. It should be added that the transverse processes of this Megaptera have been covered with cartilage, externally and half-way along the upper border, while those of the B. musculus have very little of the appearance of incomplete ossification.

32. THE AXIS.—The *anterior aspect of the body* presents articular surfaces and ligamentous markings corresponding to those above described on the posterior surface of the atlas. The ligamentous area is not sharply marked off from the low odontoid elevation, but is discernible on comparing it with that area on the atlas. The mesial articular surface is fully as well marked off as on the atlas. It curves up to the top of the

front of the broad low odontoid, with rather a narrower ending than the corresponding surface on the atlas. The furrow between it and the right lateral articular surface resembles very much the corresponding one on the atlas, in its breadth and in the character of its surface; that on the left side is very shallow, ⅛ inch in breadth at the middle, widening upwards and downwards, but well defined along its margins, and its surface resembles that of the ligamentous area rather than bone that had been covered by cartilage.

The breadth of the entire odontoid and ligamentous area is 7 inches in Megaptera, 5½ in the B. musculus. The breadth of the entire upper surface of the body is ¼ inch less in Megaptera (13¼) than in the B. musculus. The less depth of the lateral articular surfaces in Megaptera is marked.

Transverse Processes of the Axis.—The axis of Megaptera is easily distinguished from that of B. musculus by the transverse processes. In B. musculus the upper and lower processes unite to complete the ovoid ring and form a great common terminal plate external to the ring. In this Megaptera the ends of the upper and lower processes are 3 inches apart. The ends have been covered by cartilage.[1] They incline a little to each other, mainly by curvature of the upper process. Were the ring to be completed by the up-growing of the inferior process, the ring would have very nearly the same diameters as in the B. musculus.

But, even short as they are, the transverse processes of Megaptera differ materially from those of B. musculus in form and direction. The *inferior process* has the following dimensions; in B. musculus, at the narrowest part, height 3⅝ inches, thickness 1¾; in Megaptera the corresponding measurements are 2 inches and 2½. The *superior process*, on the contrary, in Megaptera exceeds that of B. musculus both in height and in thickness. Viewed antero-posteriorly, the superior process in B. musculus is only about half the breadth (height) of the

[1] The soft tissue completing the ring of the axis of a fœtal Megaptera was found by Eschricht (*loc. cit.*, p. 133) to be cartilaginous. In the 46-feet-long skeleton of Megaptera in the Brussels Museum, noticed by Professor Flower (*Proc. Zool. Soc.*, 1864, p. 416) as "a nearly adult individual," the transverse processes of the axis are noted as "short, thick, and convergent, but still with a wide space between them."

inferior, while in Megaptera the superior process is rather broader than the inferior.

Viewed from the side, the direction of both processes in Megaptera is seen to be downwards, and the axis of the incomplete foramen is seen to have that direction in a marked degree. In B. musculus the direction of the processes is nearly transverse, and that of the axis of the ovoid ring outwards and a little upwards. They differ also in the amount of the backward slope. The surfaces of the upper and lower processes in B. musculus are nearly on the same vertical plane, but in Megaptera the lower process is on a plane anterior to the upper process, partly at its junction with the body, and wholly so externally, from its sloping much less backwards than the upper process does.

The adaptations of these differences appear to be that, in B. musculus, the great breadth and flatness of the inferior process, and the two processes being on the same plane, are related to their having to support a great broad wing; and that, in Megaptera, the more backward slope of the upper process, as compared with the lower, is in correspondence with the slope of the same processes of the vertebræ behind it. The exception is rather in the less size and rounded form, as well as the less backward direction of the lower process in Megaptera. Its circumference is 1 inch less than that of B. musculus; the circumference of the upper process is 1 inch greater in Megaptera than in B. musculus. In its rounded form and free termination the lower process in Megaptera resembles the corresponding part of that process in Mysticetus much more than in B. musculus.

Spinous Process of the Axis.—The region of the spine of the axis in Megaptera is very different from that of B. musculus. In the latter there is the great square-shaped mass, formed by the two thick lateral longitudinal ridges, and in the valley between them the low median ridge, the true spinous process, scarcely rising to the level of the lateral ridges. The lateral ridges proceed backwards from the projections on which the true anterior articular processes are situated. In Megaptera the lateral ridges are low, proceeding backwards from the anterior quasi-articular processes noted above with the atlas.

The arch rises to the base of the spine, which projects about 1 inch as a median crest, extending the whole length of the arch. It has a curved form, not unlike that of the spine of the atlas, but the greater prominence on the anterior half is more marked than on the atlas. The top of the spine is 1¼ inch above the level of the lateral ridges.

Posterior Aspect of the Body of the Axis.—The greater diminution on the posterior surface of the body of the axis in Megaptera is remarkable. On the anterior aspect the total width of the body, to the outer edge of the articular surfaces, was noted above as only ¼ inch less in Megaptera (13¼ inches) than in the B. musculus. On the posterior aspect, the width of the body is in the B. musculus 11½ inches, in Megaptera only 9½. This is a change to the lesser width of the bodies of the five posterior cervical vertebræ in Megaptera compared with B. musculus.

33. THE FIVE POSTERIOR CERVICAL VERTEBRÆ.—*Bodies.*—The measurements are given in Table II. The forward diminution in *breadth* (already noted with the bodies of the lumbar and dorsal vertebræ) ceases with the 7th cervical. The breadth is then the same (8½ inches) on to the 3rd cervical, where it becomes 9¼. The forward diminution in *height* is arrested from the 1st dorsal to the 5th cervical, on which the height exceeds the 7 inches, and diminution is resumed on the 4th and 3rd cervical. The forward diminution in *length* goes on steadily along the neck, from 2¾ inches on the 1st dorsal to 1½ inch on the 3rd cervical.

[In *B. musculus* (Table III.) the forward diminution in *breadth* ceases on the 7th dorsal. From 9⅞ inches there the breadth has increased at the 7th cervical to 11¼, and at the 3rd cervical to 11⅝ inches. The forward diminution in *height* ceases at the 5th dorsal; from there to the 7th and 6th cervical the height has increased from 7 inches to 7⅞, and thence to the 3rd cervical has again diminished to 7 inches. The forward diminution in *length* is continued in the neck, from 3⅛ inches on the 1st dorsal to 2⅝ on the 7th cervical, and to 1¾ on the 4th and 3rd.]

The contrast between the bodies of the cervical vertebræ in Megaptera and B. musculus is, in Megaptera, their less breadth compared with the height. Taking the 4th cervical, these measurements are, in Megaptera, breadth 8½ inches, height 7;

in B. musculus, breadth $11\frac{5}{8}$, height $7\frac{3}{8}$. At the 13th dorsal the breadth exceeds the height in Megaptera by $1\frac{7}{8}$ inch, in B. musculus by 3 inches. At the 7th dorsal the excess is, in Megaptera 2 inches, in B. musculus $2\frac{5}{8}$. At the 4th cervical the excess is, in Megaptera $1\frac{1}{2}$ inch, in B. musculus $4\frac{1}{4}$ inches. It would best express the difference to say that it is in the increased breadth of the bodies in B. musculus. In the neck of Megaptera the bodies remain nearly the same in breadth and in height as at the anterior dorsal, while in B. musculus, from the 7th dorsal forwards the breadth goes on increasing, the height but little so. This increase of the breadth of the cervical bodies in B. musculus may be related to the greater development of tranverse processes in it than in Megaptera.

The less actual *length* of the bodies in Megaptera is seen in Tables II. and III. In Table I. the length of the neck is given as the same in Megaptera and B. musculus (19 inches). This was taken as the vertebral columns lay together. The cervical vertebræ, as now built up and standing together, have the length of 17 inches in Megaptera, in B. musculus $17\frac{3}{4}$. The five posterior vertebræ together are $9\frac{1}{2}$ inches in Megaptera, in B. musculus 11. This is without the fibro-cartilages. The five posterior vertebræ, therefore, contribute less proportionally to the length of the neck in Megaptera than in B. musculus, and may be regarded, so far, as in a somewhat more reduced condition. Regarded, however, in relation to the different total length (40 feet and 50 feet) of the two carcases, not only is the whole neck proportionally longer in Megaptera than in B. musculus, but even the five posterior vertebræ contribute to the greater proportionate length of the neck.

Inferior Transverse Processes.—These are present only on the 3rd and 4th. The angular eminence on the 5th, where the front and side of the body meet, can scarcely be termed a process. At the root they occupy nearly the whole length of the body, not nearer the front than the back, and have very little vertical expansion where they join the body. In these respects they contrast with the roots of the processes in B. musculus. That of the *third* vertebra, $3\frac{1}{2}$ inches in length, shows on its outer half the commencement of the tubercular stage by moderate expansion of the lower part of the process.

That of the *fourth* vertebra is shorter than the third by ¾ inch, and is more robust throughout, especially vertically, giving it a more rounded form. The tubercular stage is seen on its outer third. Viewed from below, the inferior processes stand out transversely. Viewed from the side, they are seen to be directed considerably more downwards than are the corresponding parts of the same vertebræ of B. musculus. The shortness of the inferior transverse processes in Megaptera, and their cessation after the 4th vertebra, indicate a much less development of the inferior intertransverse ligament in Megaptera than in B. musculus.

[In this 50-feet-long *B. musculus* the inferior processes of the 3rd, 4th, and 5th vertebræ show the root stage, tubercular stage, and nerve-groove stage (described *loc. cit.*, 1872, pp. 6 and 25), and the as yet incomplete terminal plate. The process of the 5th is, as in the other specimens, the strongest. The processes of the 6th show the tubercular stage, 2½ to 3 inches in length, beginning by a forward angular projection, and tapering outwards to a blunt point. The 7th vertebra shows only the low tubercle on the posterior half of the body.]

Superior Transverse Processes.—These differ from the transverse processes of B. musculus in commencement, length, direction, form, and in the absence of marked division into stages. The *commencement* of the process in Megaptera is more external on its upper margin than on its lower; in B. musculus it is the reverse to a marked extent. This is owing to the more outward position of the articular processes in Megaptera. On their lower margin the processes begin external to the plane of the side of the bodies (½ to 1 inch, increasing backwards), owing to the narrowness of the bodies and the greater length and obliquity of the pedicle than in B. musculus. In the latter the lower margin of the process begins internal to the plane of the side of the body on the third and 4th vertebræ, but not when the 6th and 7th are reached.

In *length* these five processes differ but little from each other (see Table V.). They have all had cartilage on the end, and terminate in blunt rounded ends. In *direction* their comparative shortness lessens the appearance of great convergence presented by B. musculus. Taking the distance between the processes from the 7th to the axis, at their roots and at

their tips, the convergence in B. musculus is from 9 inches at the roots to 2¼ inches at the tips; in Megaptera from 7 inches at the roots to 4 inches at the tips. The ends are not in contact, separated by intervals of from ¼ to ½ inch, but are nearer each other than are the processes of B. musculus at the same distance from the bodies. The process of the 5th, as in B. musculus, is the central one to which the others converge, but the 6th and 7th have not so much forward slope as in B. musculus.

In *form* the distinction between the nerve-groove stage and tubercular stage is scarcely recognisable. The whole process is more rounded than in B. musculus, standing out like a long finger, but is still somewhat flattened, surfaces forwards and backwards, especially towards the root. The greater breadth and flatness of the superior as well as of the inferior processes in B. musculus may be regarded as related to their having to support large terminal plates. The special roughnesses seen in B. musculus for the attachment of the superior intertransverse ligament, are but faintly marked in Megaptera. All this points to less necessity for binding together of the vertebræ of the neck in Megaptera. Although these superior processes might bear a ligament of considerable strength, Megaptera wants the binding of the enormously strong external intertransverse ligaments (*loc. cit.*, 1872, p. 9) which hold together, at the apex of the pyramid, the expanded terminal plates, and tie them to the vast expansion of the wing of the axis.

Comparing the superior processes with each other, the 3rd is the most slender in both Megaptera and B. musculus, but more strikingly so in Megaptera. In B. musculus they increase moderately in strength backwards from the 3rd to the 5th, and then greatly on the 6th and 7th. In Megaptera that progression is interrupted by the 4th process being as thick as the 5th on the left side, and much thicker than it on the right side. The 6th has the same robustness as the right 4th. The 7th undergoes very sudden enlargement, and, relatively to the others and to the 1st dorsal, is larger than in B. musculus. It is almost, if not quite, as large as the 1st dorsal, and presents almost as large and as thick an outer end. The 7th stands out as a strong process, and in the recess between it and the axis

are the free ends of the four intervening processes in a gradually increasing line backwards; the second 1½ inch less projecting than the axis, the 6th only a little less projecting than the 7th.

Another differential character of the superior transverse processes of Megaptera is their straightness. In B. musculus they curve upwards, so as to give the ring a decidedly concave upper boundary; in Megaptera they are almost straight from where they leave the pedicle, with a little concavity at their outer end only. The 7th begins to show a little general concavity. This straightness is seen also on the upper aspect, though with less definite outline, and contrasts with their convexity in B. musculus.

In regard to the size of the space between the upper and lower processes, it is seen in Table V. to be about the same in both, a little less in Megaptera. The distance between the ends of the two processes of the 3rd and 4th vertebræ is 5½ and 6 inches. The ends of the upper processes are on a plane posterior to those of the lower, to the following extent—axis, 2 inches; 3rd vertebra, 1½; 4th vertebra, 1 inch. In B. musculus they are on the same level, having to meet externally; but on the 6th, as the lower process stops short, the outer end of the upper process is on a plane somewhat anterior to the end of the lower process. In the fœtus of Megaptera, Eschricht found the soft tissue completing the rings behind the axis to be fibrous.

The comparison of the transverse processes in B. musculus and Megaptera would seem to show that the presence of complete processes, forming rings, is not in adaptation to the protection of the great vascular rete that occupies the space, but for the attachment of ligaments and muscles.

Articular Processes of the Five Posterior Cervical Vertebræ.—The measurements in Tables II. and III. show the much greater width apart of the articular processes in Megaptera than in B. musculus, the distance averaging about 11 to 11½ inches in Megaptera, in B. musculus about 9 to 9½, the measurements taken from the outer edge of the processes. The great increase (going forward) in width apart between the processes begins in both at the 5th dorsal, owing to the turning outwards of the processes; obtains its maximum on the 1st

dorsal in B. musculus (10 inches), in Megaptera on the 1st dorsal and 7th cervical (11½), and thence, along the neck, diminishes a very little forwards to the 3rd. This greater width apart of the articular processes in Megaptera, by 2 inches, is the more remarkable, as the bodies are narrower in it than in B. musculus by fully 2 inches. From this it results that, when the two sets of cervical vertebræ are viewed from below or from above, the sides of the bodies are seen to be considerably internal to the outer edge of the articular processes in Megaptera, and considerably external to them in B. musculus, affording a very distinctive character.

The above characters are seen in the articulated position. The following characters of the articular processes are seen when the vertebræ are laid out separately alongside each other. The articular *surfaces* are larger and ovoid in form in Megaptera, averaging 2 inches transversely by 1½ antero-posteriorly; in B. musculus they average 2 inches transversely by ¾ to 1 inch antero-posteriorly. They are larger between the axis and 3rd (in Megaptera 2½ by 2, in B. musculus 2½ by 1¼), and become smaller and more irregular backwards along the series in both. The difference in form is owing to the anterior processes projecting more in Megaptera; so that in B. musculus the anterior half of the ovoid is wanting, especially on the inner side, where the border of the process falls gradually into continuity with the anterior border of the lamina.

In Megaptera the anterior processes, from the 3rd to the 6th vertebra, are moderately convex, becoming flat on the 7th; in B. musculus the anterior processes are convex on the 3rd, 4th, and 5th, flat on the 6th, concave on the 7th. Their convexity on these three vertebræ in B. musculus is owing to their bending down towards the transverse process; while, behind the 5th, the upper edge of the transverse process comes quite up to the outer edge of the articular process.

Considering the firm binding together of the bodies by their fibro-cartilages, there can be very little movement at these diarthrodial surfaces, and most of them present irregularities of surface. But their greater extent in Megaptera would seem to indicate more movement at the articular surfaces in it than in B. musculus.

Viewed *in relation to the pedicle*, a distinctive character is afforded by lines drawn vertically up from the inner and outer borders of the pedicle. The inner line, drawn from the concavity of the border, corresponds in Megaptera to the inner end of the articular process; in B. musculus it cuts off about the inner third of the process. The outer line, drawn from where the pedicle leaves the body, would, in Megaptera, cut off the inner third or fourth of the articular surface less and less backwards, so that on the 6th and the 7th line would fall at the inner end of the process. In B. musculus the line would pass at the outer edge of the process of the 3rd, and more and more external to the processes as we go back. These differences result partly from the articular process being in part placed in B. musculus on the lamina, while in Megaptera they are placed above the pedicle, and above the root of the transverse process; and partly from the greater breadth of the pedicle in B. musculus.

Pedicles of the Five Posterior Cervical Vertebræ.—As seen in Table II., the diminution in the *breadth* of the pedicles in Megaptera, as we go forward in the dorsal region, is continued to the 6th cervical ($1\frac{5}{8}$ inch), in front of which there is very little change. The forward diminution in the *thickness* of the pedicle, from the dorsal region, ceases after the 6th cervical ($\frac{7}{8}$ inch), except on the 3rd cervical, on which it is slightly increased. The greater size of the anterior articular process may account for the pedicle of the 3rd being a little stronger than that of the three behind it, although its transverse process is the weakest.

[The much greater *breadth* of the pedicles in *B. musculus* is related to the greater size of the transverse processes they have to support. Their relation to the sides of the bodies is much the same in both, and the width of the canal is nearly the same in both; their greater width in B. musculus is gained by the greater breadth of the bodies in it. Their forward narrowing goes on from $3\frac{3}{4}$ inches on the 1st dorsal, and $3\frac{1}{2}$ on the 7th cervical, to $2\frac{1}{2}$ inches on the 3rd cervical. But their *thickness* is less than in Megaptera, $\frac{5}{8}$ inch against $\frac{7}{8}$.]

The appearance of less *height* of the pedicle in B. musculus is deceptive, owing to its greater breadth, and to the breadth and lowness of its connection with the transverse process. Measured along the middle to the middle of the anterior articular process,

the height is very nearly the same in both. The high-up commencement of the lower border of the transverse process gives a longer neck to the pedicle in Megaptera, and the inward slope of that border towards the body increases the upward and outward obliquity of the pedicle in Megaptera. That obliquity is related to the more outward position of the articular processes in Megaptera.

Spinal Canal in the Neck.—(*a*) *Capacity.*—The increase in height, with diminution in width of the canal at the 3rd vertebra, as compared with the 4th, in both Megaptera and B. musculus, is a transition to the form in the axis, in which the height is considerably increased and the width diminished. In *height* the canal increases a little backwards from the 4th to the 7th ($3\frac{1}{8}$ inches to $3\frac{3}{8}$), after which the increase to the dorsal height begins (1st dorsal, $3\frac{5}{8}$ inches). The *width* is greatest at the 6th and 7th cervical (7 inches) and 1st dorsal ($6\frac{7}{8}$ inches), and thence diminishes forwards to $6\frac{1}{2}$ inches on the 4th, and backwards along the rest of the column.

[In *B. musculus*, the *height* from the 4th to the 7th cervical ($2\frac{7}{8}$ inches) is less than in Megaptera (1st dorsal, 3 inches). The *width*, from the 4th to the 7th cervical, increases from $6\frac{5}{8}$ inches to 7; is $7\frac{1}{16}$ on the 1st dorsal, and thence diminishes backwards.][1]

(*b*) *Form.*—The somewhat higher arch in Megaptera is not obtained by greater slope of the lamina towards the spine, but rather by the lateral angles being carried higher up, and therefore less sharp than in B. musculus. In the floor of the canal the longitudinal median ridge of the bodies is seen *in B. musculus,* extending all along the neck. It begins near the fore

[1] The most capacious part of the spinal canal being in both the back part of the neck, would accord with an assumed enlargement of the spinal cord at the origin of the nerves of the pectoral fin. If so, the enlargement should be greater in Megaptera with its enormous pectoral fin. The bony canal here is more capacious in Megaptera, but only from its greater height. In the measurements of the three previously noted series of cervical vertebræ of B. musculus (*loc. cit.*, 1872, Table, p. 20) the capacity of the canal of the 6th and 7th was found not to be greater than at the 4th and 5th cervical. In one it was greatest at the 5th and 6th; in a second at the 4th and 5th; in the third, at the 6th and 7th. But considering the small size of the spinal cord (at the middle of the neck the tube of dura mater was found to be only 1 inch in diameter (*loc. cit.*, 1872, p. 5), and that the great part of the bony canal is occupied by rete mirabile, correspondence between any special enlargement of the cord and the capacity of the bony canal can hardly be expected.

part of the axis, is 1 inch broad on the following more anterior vertebræ, and becomes less marked on the more posterior. The body is concave transversely on each side of it, so that, but for the ridge, the whole upper surface of all the bodies would be transversely concave. In *Megaptera* the median ridge is less marked. It begins at the same place on the axis, is narrow on the 3rd, mesially grooved on the 4th, less marked on the 5th, and very faint on the 7th. Transverse concavity on the upper margins of the bodies ceases on the 5th, and on the 7th the whole upper surface of the body is convex transversely (continued on the dorsal), presenting a marked contrast to the 7th of this B. musculus.

Spinous Processes of the Five Posterior Cervical Vertebræ.—The 3rd and 6th have been injured. The 4th ($\frac{3}{8}$ inch in length) and the 5th ($\frac{3}{4}$ inch) are a little longer, the 7th ($1\frac{1}{2}$ inch) a little shorter than in B. musculus. The 7th has a backward direction in Megaptera, like the anterior dorsal spines; in B. musculus it is nearly straight up, like that of the 1st dorsal. After the 4th, the spines in Megaptera have a more unfinished appearance than those of the B. musculus.

Laminæ.—The laminæ are necessarily longer (transversely) in Megaptera, from the farther-out position of the articular processes, but the chief differential characters are their breadth (antero-posteriorly), filling up the spaces, and their much greater thickness and convexity on the upper surface, in Megaptera. The convexity appears as a rough bulge occupying about the middle half of the lamina transversely, and the posterior $\frac{3}{4}$ of the breadth. The same is seen on the 1st dorsal and less on the 2nd. These prominences seem to correspond to the anapophysial processes previously described in B. musculus (*loc cit.*, p. 24, and fig. 3, 1872), but they are not prolonged behind the lamina. They are rough on the surface and evidently for the attachment of muscular or ligamentous structures.

The laminæ of the 3rd and 6th vertebræ have been injured from the rough usage they received in Dundee harbour, but, as far as can be judged now, the spaces have been filled up by the anterior overlapping the posterior, except on either side of the 3rd arch, although it cannot be determined how far this is from breakage of the thin anterior edge of the 3rd and 4th lamina.

On separating the vertebræ, a fossa is seen on the posterior aspect of each thickened part of the laminæ, as if the anterior edge of the lamina behind had passed into a cavity on the lamina in front. On the 5th, on which these fossæ are most pronounced, they are elliptical, 2 inches transversely by ¼ to ½ inch in breadth, the broader end outwards, at about 1 inch internal to the articular process, the narrow end 1 inch or less from the spine; depth, from ⅛ to ⅛ inch or less. They have a very distinct and raised inferior margin, which is the true lower edge of the under surface of the lamina, the fossa itself being on the thickened posterior margin of the lamina. They have not the appearance of having been covered by cartilage, but are evidently parts into which something definite has been received. On the 3rd, it is seen, on the less injured side, as a shallow depression near the spine, 1 inch in length. On the 4th, they have the length and breadth noted above on the 5th, but are divided by a median ridge into an inner and outer part, as if two parts of the lamina behind had been lodged in them. On the 6th, it is seen on the least injured side, as if divided into three parts. If the corresponding part is represented on the 7th vertebra, it is as a rough depression running along the posterior margin of the lamina, beginning at the articular process, seen on the upper aspect of the posterior margin of the lamina. So far as they are complete, there is no special thickening, or mark, on the anterior edge of the lamina behind corresponding to these fossæ.

[In the *B. musculus* there are spaces on each side of the 7th and 6th arches, wide enough to receive the hand flat, and a narrower one between the 5th and 4th. The laminæ are flat and thin compared with those of Megaptera, the anterior border of the 3rd, 4th, and 5th so thin as to be flexible. The laminæ are not nearly so thin as in the 65 to 66-feet-long B. musculus, but are thinner than in the 64-feet-long B. musculus before described (*loc. cit.*, 1872). Nor are the very marked anapophysial processes described in them present in this 50-feet-long B. musculus to any great extent. They are seen only on the 3rd and 4th vertebræ, with a mere trace on the 5th, and are short and flat. The fossæ seen on the posterior border of the laminæ in Megaptera are not present in this 50-feet-long B. musculus, but corresponding fossæ or grooves are seen, more or less, in the three more mature individuals, best marked in the 64-feet-long one, least marked in the 60½-feet-long one. They are not so sharply marked on their inferior border as in Megaptera, and lie more towards the spinous process.

Van Beneden and Gervais remark (*Ostéographie des Cétacés*, p. 132), "C'est dans la région cervicale surtout que se trouvent les différences qui séparent le keporkak de la Megaptera Lalandii." The differences which they go on to note between these two supposed different species, Megaptera longimana and Lalandii, are, so far as I can judge, not greater than those seen in the four series of the cervical vertebræ of B. musculus above referred to.]

THE RIBS.

The following table (Table VI.) shows the proportions of the ribs in comparison with those of the 50-feet-long B. musculus:—

34. TABLE VI.—*Measurements of the Ribs of Megaptera longimana and of the 50-feet-long B. musculus, given in inches.*

	Megaptera longimana.						B. musculus.					
	Length.[1]	Depth of Curve.	Breadth at Middle.	Thickness at Middle.	Angle to Tubercle.[2]	Tubercle to end.[3]	Length.[1]	Depth of Curve.	Breadth at Middle.	Thickness at Middle.	Angle to Tubercle.[2]	Tubercle to end.[3]
1st Rib, . .	41	8	4¼	1⅜	3	3	36	9	4¼	1¼	3¼	1⅜
2nd " . .	53¼	13¾	3¼	1⅝	6	1¾	50⅜	12⅝	4	1⅞	3⅜	6
3rd " . .	59	16¾	3	1⅞	4¾	2⅝	60	14⅝	3¾	1⅝	5	5¾
4th " . .	61	17¼	2⅝	2	5	2¼	63⅜	16¼	3	1¼	4⅜	4
5th " . .	62	19	2⅞	1⅞	6	2	66¾	17⅝	2⅝	1¼	5	2¼
6th " . .	68*	19 1/16	2¾	2	5¼	2	67	18⅝	2⅝	1⅜	5	2⅜
7th " . .	59¼	18⅞	2⅞	2	5⅜	2	66	17⅝	2⅝	1⅝	5	2
8th " . .	56⅜	18	2⅝	2	...	2¼	63¾	16⅝	2¼	1⅝	5	1¾
9th " . .	55	16⅝	2⅝	2	...	2⅜	61	14¾	2⅝	1¼	4¼	1⅜
10th " . .	53¼	14¾	2¾	2	...	2¾	58	13⅝	2 1/16	1 1/16	4⅜	1⅜
11th " . .	51	11¾	2	1⅞	...	2¼	54¾	11	1⅞	1⅝	4¾	1⅜
12th " . .	49¾	10	2⅛	1⅞	...	2¼	51¾	8¼	1 1/8	1⅜	3	1¼
13th " . .	49¼	8⅞	2	1⅜	...	1¼	51	5⅝	2	1	...	1¼
14th " . .	45¼	7⅞	1⅝	1⅝	...	¾	51⅜	5¼	2⅜	⅜	...	...
15th " . .	...	...	...	...	...	...	32⅜	3	1¼	⅜	...	...

35. GENERAL AND DIFFERENTIAL CHARACTERS.—*Length.*—All the ribs of the Megaptera are shorter than those of the B. musculus except the two first. The greater length of especially the first in Megaptera is considerable. The lengths taken along the outer border are, of the first rib, Megaptera 48 inches, B. musculus 44¼; of the second rib, Megaptera 65 inches, B. musculus 60. The longest rib in both is the 6th.

[1] From top of tubercle to farthest part of lower end.

[2] From top of angle to top of tubercle.

[3] Transversely, from innermost point to opposite the top of the tubercle.

* The weight of the 6th rib is in Megaptera 228 ounces, in the B. musculus 148 ounces.

Taken along the outer border the lengths of the 6th ribs are, Megaptera 80 inches, B. musculus 82.

Breadth.—The greater breadth of the *first rib* in Megaptera is on the right side only and not throughout, as the following measurements show, in inches:—

	Megaptera.		B. musculus.	
	Right.	Left.	Right.	Left.
At external neck,	3	3½	4⅝	same
At middle of upper half,	3½	3½	3¾	same
At middle,	4½	3⅞	4¼	same
At middle of lower half,	6	4½	5¼	5⅜
At 6 inches from lower end, top of sternal notch,	7⅛	5	6	6⅛
At lower end,	3½	2¾	7¼	8⅛

On its lowest 6 inches the first rib is deeply excavated anteriorly on more than half of its breadth (see fig. 18). This peculiarity belongs to its relation to the sternum. In B. musculus this notch is not present, the rib passing of full and increasing breadth in below the wing of the sternum. A shallow excavation, ½ to ¾ inch deep, is seen on the lower part of the anterior border of the 2nd rib in Megaptera.

On the 2nd, 3rd, and 4th the breadth is greatest in B. musculus. From the 7th back to the 12th, greatest in Megaptera. On the 14th Megaptera loses, being the last rib. To the eye it appears evident that in Megaptera the more anterior ribs are narrower, and the posterior ribs broader, than in B. musculus.

In *Megaptera* the external neck is broader than in B. musculus, except on the 1st and 2nd, and is the broadest part of the bone except on the 1st and last, on the 2nd and 3rd very much the broadest part; all the shafts are narrowest at their lower end except the last; the broadest part of the shafts is below the middle, on the third quarter of the bone. In *B. musculus* the broadest part of the shaft is at about the middle of the lower half; on the lower quarter of the bone the breadth diminishes downwards, except on the 5th and 6th ribs, which rather increase in breadth to the end; from the 4th to the 13th the breadth is greater at the middle of the upper half than at the middle of the bone. The ribs of Megaptera and B. musculus, therefore, differ in breadth at different parts thus:—In B. musculus, external neck narrower (except on the two first); upper half of shaft broader

than at middle; broadest part lower down, about middle of lower half, while in Megaptera it is on the third quarter of the bone; taper less towards lower end, from the 2nd to the 7th or 8th, than in Megaptera except on its first and last. The breadths of the longest rib of each, the 6th, are, in Megaptera and B. musculus respectively,—at external neck, $3\frac{5}{8}$ and 3 inches; at middle of upper half, $2\frac{5}{8}$ and 3; at middle, $2\frac{5}{8}$ and $2\frac{5}{8}$; at middle of lower half, $2\frac{7}{8}$ and 3; at 6 inches from lower end, $2\frac{5}{8}$ and $3\frac{1}{4}$.

Thickness.—The ribs of Megaptera and B. musculus differ mainly in their greater thickness in the former, becoming marked after the 2nd and continuing to the last, as seen in the 4th column of the Table. To the grasp, they are ovoids in Megaptera, becoming, relatively to the breadth, thicker as we go back, the four last ribs nearly as thick as they are broad. The measurements given in the Table are taken at the exact middle of the entire rib, which is about the thickest part, but there is not much diminution in thickness till upon the upper and lower fourths of the bone. The upper thinning becomes marked as we approach the angle, and is greater than that towards the lower end. From the 3rd or 4th to the 9th or 10th, and again on the last, the thickness to the very end below in Megaptera is very striking compared with the corresponding ends in B. musculus.

[In *B. musculus* the beam of the 2nd rib is external, the inner $\frac{2}{3}$ thin and deeply grooved on both surfaces; this along about the middle half of the length of the shaft. The 3rd rib the same, but the grooving less marked. On and after the 4th, the thickest part is at, or a little internal to, the middle of the breadth, with about equal sloping on each side of it. The 13th becomes thin externally, the 14th and 15th are thin across their whole breadth. On the typical ribs the beam projects chiefly on the external surface, beginning at the angle, passing obliquely to about the middle of the surface, and ceasing near the lower end. The internal part of the upper half of the shaft is strengthened by a minor beam seen on the inner surface, beginning at the inner border and reaching obliquely outwards to the main beam. The inner surface, taken generally, is flatter than the outer surface, especially along the lower half. At the posterior border a special *sub-costal groove* and ridge are present towards the lower end, from the 5th to the 12th, beginning 10 to 12 inches from the lower end of the rib and extending upwards for about the same

distance; best marked on the 9th, 10th, and 11th, where it is as broad as the little finger.]

In *Megaptera* the course of the beam is the same as in B. musculus on both surfaces, but is rendered much less distinct by the greater general thickness of the bone on each side of it. On the 2nd and 3rd ribs the beam has already reached to about the middle, and there is scarcely any of the grooving to its inner side which is so strongly marked in B. musculus on the 2nd and 3rd, and even from the 4th to the 7th above their middle. A trace of the sub-costal groove is seen from the 3rd to the 10th, from 6 to 12 inches in length, a little above the junction of the lower and middle thirds of the bone, somewhat higher up on the 10th. Where it is sharp-edged it has the breadth of a goose-quill.

Curvatures of the Ribs.—Although these ribs are more simple than in most mammals, the four curvatures are seen and differ in Megaptera and B. musculus—(1) The curvature of the axis, enclosing the chest, is seen in the second column of the table. Except on the 1st rib, in which it is 1 inch less ($1\frac{1}{2}$ on the left side), the depth of the curve is seen to be greater in Megaptera than in B. musculus along the whole series, thus giving Megaptera a wider thoracic cavity. It increases to the longest rib in both. The greater curvature in Megaptera is most striking on its last two ribs.

Of the minor curvatures in (2) that of the *borders*, giving the sigmoid form, the differences are not very marked. On the outer border the concavity below the angle is seen in B. musculus from the 1st to the 11th, owing to the greater prominence of the angle; in Megaptera on the 2nd and 3rd, and again on the last four, but not much. On the lower third, the concavity on the outer border, with convexity on the inner, is seen in Megaptera from the 2nd to the 6th; in B. musculus only on the last four; on the 13th, exceptionally well, the shaft of this rib presenting a decidedly sigmoid form. These curvatures are greatly exaggerated on the last rib of the Megaptera, and usually on the last rib of B. musculus, as noted below.

(3) *Curvature on the Surfaces.*—This is much more marked in Megaptera, both above and below. In Megaptera the upper

part of the rib is much bent forwards at the angle, while the whole shaft is bent with the concavity backwards, giving a marked sigmoid form when the rib is seen edgeways. In B. musculus there is, above, only a gentle bend forwards on the upper $\frac{1}{4}$, without any rapid bend at the angle; and below, a well-marked bend backwards on the lower $\frac{1}{4}$ of the shaft, giving the sigmoid form. When the 6th ribs, the longest, of Megaptera and B. musculus are laid together on the floor, resting on their outer border, the upper end rises, in Megaptera 10 inches, in B. musculus 6 inches; and the lower half of the shaft forms an arch $2\frac{1}{2}$ inches deep in Megaptera, $1\frac{1}{2}$ deep in B. musculus. The rise at the upper end in Megaptera begins about 15 inches from the articular end, but much the greater part of it takes place at the angle, about the middle of that distance. The rise in B. musculus is by a gradual sweep along the upper $\frac{1}{4}$ of the bone, not marked at any particular place. If the external neck be now made to lie level on the floor, the whole shaft in Megaptera rises as an arch 13 inches high at the middle; that of B. musculus as an arch 5 inches high, and along its lower $\frac{3}{4}$ only, highest at $\frac{1}{4}$ from the lower end. When these two ribs are turned on their outer surface, and the external neck laid level on the floor, the lower end rises from the floor, in the Megaptera rib 37 inches, in the B. musculus rib only 9 inches. The differences are also well seen when the two ribs are made to stand together vertically. These curves of the surface are much better marked on the anterior half of the series (except the 1st) than on the posterior half.

(4) *Torsion.*—The torsion or twist of the plane is seen below on the lower half of the shaft; above, on the upper part at the angle, and specially at the articular end. The *lower torsion* is very evident in B. musculus, the inner margin on the lower half of the shaft twisted forwards, so that the surface which is anterior above now looks outwards. In Megaptera, the greater thickness of the shaft renders this torsion less obvious, but it is greater than in B. musculus. The *upper torsion* is much greater in Megaptera than in B. musculus. Along with the upper bend forwards on the surface, the plane is at the same time twisted, the inner (now lower) border back-

wards. This twist is in the opposite direction to that of the lower half of the shaft, but to a less extent. The torsions thus accompany the two bends on the surface. The effect of the upper bend and torsion is to give the upper part of the rib a more horizontal direction inwards, and to render the plane of its surfaces vertical; the effect of the lower torsion is to make the lower half of the shaft face more outwards as it sweeps obliquely back along the thoracic wall. These differences in the bend of the surfaces and in the torsion, between Megaptera and B. musculus, would seem to be adaptations in Megaptera to a more abrupt change from the transverse direction of the upper part to the oblique direction of the shaft.

The special *torsion at the articular end* is a rapid twist of its lower part backwards, affecting also the lower part of the inner half of the external neck. The result is that the articular end, where it meets the transverse process of the vertebra, is directed downwards and backwards, decidedly so in B. musculus, moderately so in Megaptera.

The Last Rib.—This rib in Megaptera has the very undulating character usually seen in the last rib in B. musculus and other finners. This is but an exaggeration of the curvatures of the other ribs, with, if the rib is long enough, the addition of a third curvature to the sigmoid form. On the posterior border, after the slight concavity external to the articular end (there is no angle), there is the great convexity occupying about the upper $\frac{2}{5}$ of the bone; then a wide concavity, occupying about the middle $\frac{1}{3}$ of the bone. These with corresponding curvatures on the anterior border, complete the sigmoid form (like the human clavicle, but not so much bent as it), and there is only that in the 15th rib of this B. musculus, and in the last rib of my B. borealis. But in this Megaptera a third curve is present on the lower $\frac{1}{3}$ of the bone, convexity behind. The hinder margin thus presents two convexities and one concavity, the anterior margin two concavities and a convexity. The 13th rib, with much less of the upper two bends, shows the third of these bends more typically, owing to the tapering of its posterior margin towards the end. The want of this tapering on the last rib (breadth of end $2\frac{1}{8}$ inches, of end of 13th, $1\frac{1}{2}$ inches), with a slight bend

back at its broad lower end, gives the last rib, of the right side, the appearance of having a short fourth bend on its lower six inches. The left 14th rib has not this, and the middle of its three curves is less pronounced than the corresponding curve on the right.

[The 15th rib of my 64-feet-long *B. musculus* (72 inches long) shows the three curves on a great scale. There was a 16th pair of ribs in that B. musculus (this *Journal*, 1871, p. 115) loose in the flesh (right 30 inches, left 22 inches long), which the 15th, the last, of this 50-feet-long B. musculus closely resembles, except that the latter has more of the sigmoid form. The upper 9 inches taper, the upper 6 inches rounded, to a point half the size of the end of the little finger.]

36. VERTEBRAL ENDS OF THE RIBS.—The modifications of these in Megaptera will be better understood after observing them in B. musculus.

[*In B. musculus.*—The 1st rib of this B. musculus has no beak.[1] The 2nd and 3rd ribs have a long capitular process or beak. This process, and the ligament which prolongs it to the body of the vertebra in front, together represent the neck and head of the complete rib of the toothed Cetacea and of most mammals. Above the base of the beak is the well-marked tubercle by which the rib articulates with the transverse process of its vertebra, and between this and the angle is the moderate constriction which may be termed the external neck. The common error of calling the end of the ordinary or beakless ribs of the whalebone whales the "head," and the constriction external to it the "neck," was emphatically remarked on long ago by Eschricht (*loc. cit.*, p. 137). The rapid shortening of the capitular process after the 3rd gives the ribs first a sloping and then a rounded end. The 4th shows a considerable slope to a sharp point; after the 4th there is less and less slope, and the angle below is rounded off, so that the most projecting part of the end is not its

[1] In my 60½-feet-long B. musculus the 1st pair of ribs have as well-marked and as long a beak as the 2nd pair have (this *Journal*, 1872, p. 47). In my 64-feet-long B. musculus the beak occurred on the left side as a separate piece, articulated by cartilage to the lower part of the broad end (this *Journal*, 1871, p. 116, and fig. 4, Plate VII.). The condition on the right side could not be ascertained. In this 50-feet-long B. musculus, the end of the 1st rib is broad and rounded, the lowest part, from which a beak would have proceeded, somewhat rounded off below and thin, and without any appearance of a movable beak having existed. The cartilage-covered surface extends over the whole height and breadth of the end: height 5¾ inches; breadth above, 1¼ inch, at middle ¾ inch, at lower part ¼ inch. Upper ¾ convex backwards, lower ¼ concave backwards. The occurrence of a beak on the 1st rib in B. musculus appears to be a matter of ossification or of variation.

lowest part. The sixth column of the Table shows the amount of the slope from the top of the tubercle to the most projecting part of the end.

The *articular surface* or cartilage-covered area[1] begins at the top, or, it may be, a little external to the top of the tubercle. On the 1st rib it occupies the whole end. On the 2nd and 3rd it occupies the inward slope of the tubercle, or what might also be called the broad part of the beak, for 4 to $4\frac{1}{2}$ inches; leaving a narrow beak proper, 5 inches long on the 2nd rib, 4 inches long on the 3rd rib. On the 4th rib the articular area extends over the whole sloping end, and on the ribs behind the 4th goes also a little below at the rounded-off part.

Adaptation of the Ribs to the Fossæ on the Transverse Processes.—It is not easy at first to see how the two somewhat narrow surfaces are adapted, the rib-ends being mainly vertical, the fossæ mainly antero-posterior in direction. The measurements of the end of the 7th rib are—height, $3\frac{3}{4}$ inches; breadth, upper part 1 inch, at middle $1\frac{1}{4}$, lower part $1\frac{5}{8}$. Those of the fossa on the 7th transverse process are—antero-posteriorly 4 inches, vertically 3, depth $\frac{3}{4}$ inch. If a middle rib be so placed that the long axis of the two surfaces shall correspond, the rib will be nearly horizontal. The mode of articulation, by fibrous cushion, may render exact adaptation of surfaces less necessary than in the case of diarthrodial joints, but the adaptation becomes evident on close examination. If the 7th rib is placed naturally, the lower end carried back to about opposite the 3rd transverse process behind its own, the articular end is seen to be directed downwards and backwards at an angle of about 25°, and to fit against the anterior $\frac{1}{2}$ or $\frac{2}{3}$ of the costal fossa. That is the part on which the fossa is buttressed by the thick ridge bounding it in front, thus offering resistance to the rib, and only the anterior $\frac{1}{2}$ or $\frac{2}{3}$ of the fossa have been covered with cartilage. The cartilage has been continued down upon it from the end of the transverse process. When the 12th is reached the whole area is cartilaginous, being placed on the end of the transverse process. But the rib is longer, vertically, than the fossa. Part, about $\frac{1}{4}$ or $\frac{1}{3}$, projects above the fossa, and, corresponding to this, is the concavity on the extreme edge of the transverse process, above the anterior $\frac{1}{2}$ of the costal fossa. The rounded-off part below may project under the fossa.

Looking now to the exact form of the articular end of the rib, the terminal torsion is seen to give it the downward and backward direc-

[1] The parts which have been covered by cartilage are easily recognised by their roughness and perforations. The costo-transverse articulation in finners appears to be, not by regularly formed diarthrodial joints, but by fibrous cushion. Within this I have found an irregular synovial cavity (this *Journal*, 1872, p. 48), but in B. rostrata I found no synovial cavity at any of the costo-transverse articulations. The cartilage on these tubercles and ends may be only the growing cartilage of the end, but it may be regarded as also articular in function.

tion, which is increased by the lower part being prolonged backwards into a blunt point. Two parts may be recognised—the upper, sloping upwards and outwards, is seen in the end view to face obliquely backwards, to be nearly vertical, and to be separated from the chief part by a gentle concavity, reaching upon it from the posterior concave margin. The part thus marked off appears to be that which projects above the fossa. The lower and chief part faces inwards, is more decidedly convex antero-posteriorly than the upper part, and has the oblique direction downwards and backwards. This lower part of the articular surface, as seen in the end view, is pointed below on the first three ribs; from the 5th to the 8th broadest below; on the next three the terminal torsion is so much diminished that the point of the lower part is downwards rather than backwards; on the 12th, 13th, and 14th the end is rounded, but greatest vertically.]

In Megaptera.—As compared with those of B. musculus, the most striking difference at the vertical end of the ribs in Megaptera, behind the 3rd, is the lowness and rounding off of the angle. The concavity between the tubercle and angle, on the external neck, is much less, is very slight after the 7th, and after the 9th or 10th is not present. The gentle elevation corresponding to the angle in B. musculus diminishes and disappears at the same stages of the series. The slightness of the constriction is owing also to the filling up of the external neck, the upper border of which, on the anterior seven, slopes a little upwards to the low angle. This gives the upper 12 inches or so of the rib a greater bend down than in B. musculus, and a broader external neck compared with the breadth of the shaft. This direction of the upper part of the rib and the lowness of the angle may be considered as related to the upward direction of the transverse processes, in below the ends of which they are received, although that direction of the transverse processes is continued farther back on the series.

The *first* rib has a rounded top, from the low angle inwards, tapering downwards and inwards to a blunt point. The inner half (3 inches) of this may be assigned to the beak (best marked on the left rib—see fig. 18), much turned back on its last 1½ inch; but there is no distinct tubercle, and only the blunt point, about 1 inch thick, has been covered by cartilage. The *second* rib has a prominent tubercle, the end sloping obliquely downwards and inwards, giving a broad triangular beak, 1¾

inch in length. The whole of this sloping end, 5 inches, has been covered by cartilage, as all the ends behind this have been. The *third* rib has rather more slope than the second.

The extent to which the lower part of the ends project inwards beyond the upper part at the tubercle is seen in the sixth column of the Table. It continues to be about 2 inches back to the 12th. The 2nd and 3rd ribs cannot be said to have a beak in the sense that these two ribs have in B. musculus, or even as the 4th of B. musculus has. After the 7th the slope is greater in Megaptera than in B. musculus, as seen in the Table. The remark of Van Beneden and Gervais that "la troisième surtout et la quatrième different des autres par une tête distincte" (*op. cit.*, p. 127) does not apply to this Megaptera.

Although, as seen in the end view, the articular ends of the ribs are directed less downwards and backwards than in B. musculus, the terminal torsion, affecting the inner half of the external neck and the end proper, is very marked. The twist back of the lower part of the articular end is well seen when the series of ribs are laid with the posterior surface upwards. On the first four there is both bending back of the inner part of the external neck and twisting back of its lower edge. From the 5th to the 8th there is only the decided twist; on the next two less twist; and on the last four more. The twist back of the lowest part of the articular end in some (4th to 7th on right side, 4th and 5th on left side) runs on to a projection like the end of a finger. This projection is marked on the left 5th and 7th, ½ to ¾ inch long; on the 5th it is like the end of a thumb; on the 7th like the end of a little finger. This projecting cone is not seen in the front view of the rib, and has not been covered by cartilage. It may be regarded as a rudimentary beak, but it is irregular and not symmetrical.

Adaptation of the Ribs to the Fossæ on the Transverse Processes.—The distinction of the articular end of a typical rib into upper and lower parts is more marked in Megaptera than in B. musculus. The whole area is more bent, almost kidney-shaped. The concavity, going on the surface from the most concave part of the posterior margin, marks off about the upper ⅓. This

part is curved backwards, is much rounded off as it ascends, and faces obliquely backwards, while the lower part ($\frac{2}{3}$) faces inwards, and is more convex in both directions. When the rib is applied naturally to the vertebræ, the concavity on the articular end corresponds to the fore part of the upper boundary of the fossa; the upper part rises above the fossa, curving towards the back part of the upper edge of the fossa, but, as the outer edge of the transverse process is thick (1 inch at the middle, more in front, less behind) the rib does not seem as if it had risen above the level of the cartilage with which the process has been tipped; and the lower $\frac{2}{3}$ of the rib, more ball-like, occupies the anterior part of the fossa, the axis corresponding to that of the fossa, the direction downwards and backwards. The measurements of the end of the 7th rib are—height, almost 4 inches; breadth, below middle, $1\frac{5}{8}$. Those of the fossa on the 7th transverse process are—antero-posteriorly, at middle, $2\frac{3}{4}$ inches externally, 3; vertically, 3; depth, $\frac{1}{2}$ inch. The end of the 10th rib is $1\frac{7}{8}$ inch broad below the middle; the 10th fossa, antero-posteriorly, $3\frac{1}{4}$ inches; vertically, 4; depth, $\frac{5}{8}$ inch. But the edges of the fossæ are not completely ossified. The fossa faces downwards, and also outwards and backwards, the end of the rib upwards and inwards. The more sloping form of the ends of the ribs in Megaptera (from the less projection at the top) than in B. musculus corresponds to the more inwardly elongated direction of the fossæ in Megaptera. The articular ends are all broader in Megaptera than in B. musculus. No part of the costal fossæ in Megaptera appears to have been covered with cartilage.

The different form of the costo-transverse articulation in Megaptera, compared with B. musculus, has the result that there is more extensive contact of the opposing surfaces in Megaptera. The fossæ are more elongated vertically or transversely, and, spoon-like, receive a broader head. This difference may have reference to the much greater massiveness of the rib. But dissection of the ligaments and of these parts in their natural relation will be necessary for a complete explanation of the differences.

STERNUM.

37. TABLE VII.—*Measurements of the Sternum,* given in inches.

	Megaptera.	B. musculus, 50 feet long.
1. Length, ...	11⅛	12
2. Breadth, ...	11	18¼
3. Length of wing, transversely from where it joins the body, ...	2¼	7
4. Breadth of wing, at the end, . . .	2⅝	4½
5. ,, ,, at the middle, . .	3½	3½
6. ,, ,, where it joins body, . .	4½	4½
7. Length of cervical process, . . .	4	8
8. Breadth of ditto at its base, . . .	7	5¼
9. ,, ,, at its middle, . . .	5¼	3½
10. Length of posterior process, from level of the wings, ...	3½	5¼
11. Breadth of ditto at level of the wings, . .	6	5
12. ,, ,, at its middle, . . .	2¼	2½
13. Thickness of the beam between the wings, at middle line, ...	2	1½
14. Thickness at midway to end of wing, . .	1½	1
15. ,, at end of wing, . . .	1¼	½
16. ,, at middle of posterior process, .	1¾	1¼
17. ,, of cervical process at middle, . .	1½	½
18. ,, of anterior edge at middle, . .	¾	⅛
19. ,, ,, ,, at middle of side, .	½	sharp
20. ,, at notch between wing and cervical process, ...	sharp	sharp
21. Depth of ant.-post. concavity of under surface, .	1	1
22. Depth of transverse concavity of the upper surface, ...	1¼	1½
23. Weight of the sternum, in ounces, . .	31⅝	40⅛

38. CHARACTERS IN COMPARISON WITH THOSE OF B. MUSCULUS. —The form of the sternum is shown in fig. 18.[1]

To understand the differences of form presented by the sternum in Megaptera and B. musculus it is necessary to con-

[1] For remarks on the interpretation of the sternum in Fin-Whales, the essential and non-essential parts, and the variation of the latter, with a drawing (fig. 4) showing its two places of articulation with the first rib, I may refer to my paper on B. musculus in this *Journal,* vol vi., November 1871. Reference may also be made to the figure given by Eschricht (*loc. cit.*, p. 139, fig. 47), showing the true relation of the sternum to the first ribs in a fœtal Megaptera, with his remarks on that point. Also to the figures of the sternum in B. musculus, B. borealis, and B. rostrata by Professor Flower (*Proc. Zool. Soc.*, 1864, p. 393). The sternum of the Fin-Whales is so liable to variation according to age and individual peculiarity, that care must be taken in attaching importance to the form presented by any individual specimen.

sider the very different proportions of the anterior aperture of thorax in these two species. This is seen if the first pair of ribs are laid at the natural distances from each other above and below. In Megaptera the vertical diameter of the ring (from the top of the ribs to the anterior border of their lower end) is 32 inches, the greatest transverse diameter 28 inches; in B. musculus the vertical diameter is 28 inches, the greatest transverse diameter 35. Thus in Megaptera the width is 4 inches less than the height, while in B. musculus the width is 7 inches greater than the height. The contrast is still greater on the lower part of the ring, the greatest width being above the middle. This difference appears to determine the form of the sternum in the two species. The sternum of B. musculus could not be fitted between the naturally-placed ribs of Megaptera; the outer ⅓ or ½ of the wing would have to lie upon the rib. The narrowness of the space between the first pair of ribs in Megaptera requires a short-winged sternum, and the more oblique course of the lower end of the rib is a reason why the hinder edge of the wing should slope to the posterior process instead of passing horizontally inwards. So in B. musculus the wide ring requires a wide-winged sternum, and the nearly horizontal direction of the hinder edge of the wing is in adaptation to the nearly horizontal direction of the anterior border of the lower end of the rib. These different relations also influence the position of the marks for the terminal costo-sternal articulation, and require the posterior process of the sternum to be longer in B. musculus.

The reasons for most of the differences seen in the table of measurements (Table VII.) of the sternum in the two species are now evident. Its somewhat diamond-shape in Megaptera is owing to the shortness of the wings, and to their sloping to a short posterior process; the form of a cross in the B. musculus, to the long wings and the long posterior process. The greater massiveness of the ribs in Megaptera requires the sternum to be thicker in it than in B. musculus.[1]

In Megaptera the *cervical process* is very broad, and is in an

[1] The weight of the first rib is—in Megaptera, right 182 ounces, left 168; in the B. musculus—right 110½ ounces, left 110. But the left rib in the B. musculus has a broader sternal end than the right.

unfinished condition, the subcartilaginous border, ¾ inch thick at the middle, becoming narrower on the sides to within an inch of the base, where the edge becomes thin and completed. There is no indication of bifurcation at the front.[1] It is bent downwards very much at its base, this being the sole cause of the antero-posterior concavity of the inferior surface of the bone. On the upper surface the cervical process is rather suddenly bent downwards at the middle, rendering it convex, to which the forward thinning of the process also contributes. The moderate longitudinal convexity on the posterior half of the upper surface of the sternum is owing to the greater thickness of the beam between the wings, not to any bending down of the posterior process. It may be noted that the concavity on the border between the cervical process and the wing is not quite so deep on the left side as on the right.

39. RELATION OF THE STERNUM TO THE FIRST RIB.—The macerated bones alone would be very apt to mislead in the articulation of the skeleton. As Eschricht has shown with his usual

[1] The variation in this respect in the fin-whales is great. In my 35-feet-long *B. borealis*, the cervical process, after a length of 1½ inch, has bifurcated for half an inch, ossifying into a large undivided plate of cartilage, 2 inches in length by 4 in breadth. In the 50-feet-long *B. musculus* the cervical process, 3½ inches long, shows no appearance of past or coming bifurcation. In the figure given of B. musculus by Professor Flower (*loc. cit.*) the wings and cervical process form one great irregular semilunar plate with no sign of bifurcation, present or obliterated. In a sternum in my possession, found on the shore, which appears from its other characters to be that of B. musculus, the anterior process is very like that in the figure given by Professor Flower, except that there is a great median fissure, about 5 inches deep by 1 inch wide, nearly closed in front. In my figure of the 64-feet-long B. musculus (*loc. cit.*, 1871), the small foramen is so far back that it might be attributed to the position of a blood-vessel rather than to a former bifurcation of the bone. In two figures of the sternum of B. musculus given by Van Beneden and Gervais (*loc. cit.*, pl. xii.-xiii. figs. 14), one of them from a young animal, it is bifurcated anteriorly. The same authors give diagram figures of the sternum of *Megaptera* (*loc. cit.*, p. 128), showing a deep bifurcation closed in to form a foramen, and then the foramen obliterated. In their figure of Megaptera Lalandii (Pl. ix. fig. 5) the bone is widely bifurcated for more than half of its entire length, and they speak of the sternum of Megaptera longimana and Megaptera Lalandii as "assez semblable" (p. 134). The sternum of this Megaptera would, to all appearance, never have bifurcated, nor is there any sign of a filled-up aperture. The smooth inferior surface shows the blood-vessel grooves and perforations radiating from the middle thick part on the posterior half of the bone (the perforations towards the thick part), outwards on the wings, and forwards, symmetrically and undisturbed, on the cervical process.

care, the rib lies behind the wing of the sternum. The adaptations in the developed bones present several points of interest.

[To understand these in Megaptera it is necessary to refer to the adaptations in *B. musculus*. As seen in my figure of the parts, still in their natural connection (*loc. cit.*, 1871), there are two places of articulation—(1) the *lateral costo-sternal joint*. The end of the wing, covered by cartilage, is joined on its posterior edge by ligaments to the anterior border of the rib, where a rough mark is seen. (2) *Terminal costo-sternal joint*. The end of the rib advances towards the posterior process of the sternum, and the short cartilage belonging to the anterior part of the end of the rib is joined to the sternum by ligament. The rough mark for this articulation is very evident in the 50-feet-long B. musculus, on the angle between the wing and posterior process, and on the anterior half of the side of the process, which is specially broadened at this part. The great length, transversely, of the wing of the sternum in B. musculus gives room for a considerable space between the lateral and terminal joints. Viewing the end of the rib in the 50-feet-long B. musculus, it is seen to be divided into three parts—an anterior, 1½ inch thick; a narrow middle part, ¼ to ½ inch thick; and a posterior part, ¾ to 1 inch thick. In the 64-feet-long B. musculus the narrow middle part is a sharp-finished edge, the anterior and posterior parts broad, and each covered by cartilage. The anterior cartilage is at the terminal costo-sternal joint, the posterior cartilage is free and non-articular, and is a long way behind the sternum. The narrow middle part is the most projecting part of the rib, the free border receding from it, covered by the posterior cartilage.

In my *B. borealis* the soft parts here have been preserved, and throw light on the transition from B. musculus to Megaptera. Externally is seen the lateral costo-sternal articulation, as in B. musculus, the cartilage belonging to the sternum. Internally, after a short interval, owing to the shorter wing, the cartilage, which has been detached from the rib, is, like the end of the rib itself, 6 inches in breadth, and almost separated by a narrow middle part into an anterior and posterior part. The anterior and smaller part, 1½ inch in length, close to the sternum, is joined to it by ligament, to the angle formed by the wing and a special projection from the side of the base of the short posterior process; the posterior part, 2½ inches in length, is joined to the fibrous membrane which fills up the great gap (5 inches deep) behind the sternum, and between the greater part of the free ends of the first pair of ribs. The end of the rib recedes behind the narrow middle part, but the cartilage that covers it projects internally, to the extent of 1½ inch posteriorly, and thus gives the whole cartilage of the end of the rib a deeply notched or scooped-out form, obliquely, resembling the scooped-out end of the long rib in Megaptera.]

There is no evidence of the presence of two joints in Megaptera, but rather of one continuous oblique ligamentous connec-

tion. The end of the wing of the sternum has been covered by cartilage; the surface, 2⅝ inches by 1¼, facing outwards, with a little obliquity upwards and backwards. The rough mark for the ligamentous attachment, seen best on the left side, is on the oblique posterior border of the bone, formed by the hinder edge of the wing and the side of the broad base of the posterior process. It is 4½ inches in length, ¾ inch broad externally, narrowing gradually to ⅛ inch at the inner end. It has not been covered by cartilage. In contrast with the nearly rectangular recess between the wing and the posterior process in B. musculus, this part in Megaptera is thus filled up, giving an oblique posterior border to the bone, and contributing to its diamond form. The ligamentous mark does not extend back upon the narrow part of the posterior process, on which a sharp edge separates, for the last 2½ inches, the flat upper surface from the convex side of the process. But the ossification here is not complete on the right side. On the right side of the upper surface there is a sub-cartilaginous area, 3¾ inches in length by ¾ inch broad, extending to the very point. Further ossification of this cartilage backwards might have elongated the process, and further outward growth of its anterior part, and of the neighbouring part of the wing, would have filled up the border on the right side to the same extent as on the left. The partial concavity or oblique recess behind the wing on the right side corresponds to the presence of a greater projection on the anterior angle of the rib on the right than on the left side.

[In the *B. musculus* the rough mark for the terminal joint extends for 2½ inches on the wing and for 3½ on the posterior process, to the part where the process becomes considerably narrower, 2 inches from the point. The part of the mark situated on the process is much broader (1¼ inch) as well as longer than the part on the wing. On the left side the side of the process is quite flattened by the mark, and the recess between the process and the wing is deeper than on the right side. The asymmetry here may be related to the greater breadth (by nearly 1 inch) of the left than the right rib, at the end. On the hinder border of the wing there is an interval of 2½ inches between the mark for the internal joint and where the outer end of the wing begins to be sub-cartilaginous. The interval, however, is rough, as if it had attached a ligament. The first rib shows a distinct rough elevation on its anterior border, for the lateral costo-sternal articulation, beginning 4 to 5 inches from the end of the rib and

occupying 3 to 4 inches. This corresponds to the hinder slope of the outer end of the wing of the sternum.]

In Megaptera there is no separated mark on the rib indicating a distinct lateral costo-sternal articulation, simply the border of the rib is thick and rough for its last 7 to 8 inches, in marked contrast to the character of the border of the rest of the rib. This rough part extends 2 to 3 inches farther up the rib than the level of the fore part of the end of the wing of the sternum, as placed in fig. 18.

This border of the rib, on the right side, terminates in a prominent angle or process, the end of which shows a sub-cartilaginous surface, 1½ inch by 1 inch. The mode of articulation I infer to have been by continuous ligamentous attachment, externally, to the last 7 or 8 inches of the rib and to the cartilage on the terminal process of this border of the rib; internally, to the cartilage of the wing of the sternum and to the rough mark on the hinder border of the wing and side of the base of the posterior process. On the left rib there is no terminal process to the anterior border of the rib, simply a rounded-off angle, without thickening, but it appears to have been covered by cartilage. As shown in fig. 18, the left first rib is shorter at the lower end than the right by 1¼ inch.

Whether the wide oblique notch in the end of the first rib is exceptional in this Megaptera I have not the means of determining. The edge is thin, and as if finished on the right rib, but on the left a thin strip of cartilage appears to have been continued on the anterior part of the notch. The notch, or excavation, is on the right rib 4 inches in length, ¾ inch in depth; on the left rib 5 inches in length, ⅝ in depth. The projecting end of the rib behind the notch is 3 inches in breadth, 1 inch in thickness towards the posterior end, and has been covered with cartilage. The end of the rib, therefore, has, as in the adult B. musculus, two cartilages—the anterior, by which it articulates with the sternum; the posterior, a long way behind the sternum. Between these, in the adult B. musculus, is a thin finished edge of bone. In Megaptera this thin part is still less developed, so that there is a wide notch between the parts bearing the posterior and the anterior cartilages. But, further, in Megaptera the rib stops short on its anterior border several

inches external to what would be its end in B. musculus, giving the notch its outward obliquity. Prolongation of this border would have carried it upon or behind the point of the posterior process of the sternum. It therefore stops short when it arrives below the wing. Thus the narrowness of the anterior aperture of the thorax and the sloping direction of the rib account for these modifications of the end of the first pair of ribs, as well as for the form of the wing and posterior parts of the sternum, and for the difference in the mode of articulation, as compared with B. musculus.

[The very different proportions of the sternum in the *B. musculus*, compared with Megaptera, are seen in the measurements in the table (Table VII.). The wings are very long transversely, and more expanded near the end than at their middle; the posterior process is long and bent downwards, more than the cervical process is. The cervical process is much narrower than in Megaptera. The whole bone is thinner. The parts of the edges the ossification of which is unfinished, are, the outer edge of the wing, ¼ to ½ inch thick (the posterior slope of the end thicker than the anterior, the surface facing obliquely upwards); part of the point of the posterior process; and parts of the anterior convex border of the cervical process, thinnest ($\frac{1}{12}$ inch) at the middle (the most projecting part), a little thicker (⅛ inch) on each side. Along the posterior ⅔ of the cervical process the border is quite sharp and finished. It is not evident how this sternum could bifurcate forwards, or how their thin edges could grow so as to fill up the great hollow between the wing and the cervical process.]

The Chevron Bones.

40. Characters in Comparison with those of B. Musculus.—The chevron bones in this Megaptera are 10 in number, the first and the two last in separate halves. The number in the B. musculus is 13, in the B. borealis 15. It is easy to distinguish those of Megaptera from those of the other two finners. As seen in the table of measurements given below (Table VIII.), the arch in all of them in Megaptera is much wider at the middle than at the top, the space having the form of the lower ⅝ of an ellipse or of a rather pointed oval.

[In *B. musculus* the space in the first three is a wide triangle, 4 inches deep, 3½ across, the laminæ not coming at all towards each other at the top. On the 4th, they begin to approach a little at the top, rendering the space a little narrower there than a short way below, and this increases backwards, but not so much as in Megaptera

until we reach the 11th and 12th of B. musculus, which in this respect closely resemble the 7th and 8th of Megaptera.]

This approximation of the lamina above results from the greater breadth of the *articular surface* in Megaptera. The measurements of this surface on the 4th are, in Megaptera, breadth 2 inches, length 5; in B. musculus, breadth 1⅝ inches, length, 4½. The surface in Megaptera is elliptical, with the greatest bulge on the inner side. It is bevelled before and behind so as to present two facets; the anterior rests on the vertebra to which the chevron bone belongs, and is the more flattened of the two; the posterior rests on the intervertebral disc; in Megaptera it could not reach the vertebra behind, owing to the great length of the discs.

[In *B. musculus* the articular surface, besides being narrower, has a different form, the inner side concave on the three first, nearly straight on the next two, convex behind on the next three, and on the four posterior the surface becomes elliptical but not so broad as in Megaptera. The posterior facet, separated from the anterior by a middle rounded part, may rest on the vertebra behind. The *arch* (included space) is about as large as in Megaptera.]

The *spines* are but little developed in height or in breadth (antero-posteriorly) compared with those of B. musculus. This is, at least in part, owing to the less advanced ossification in Megaptera, but the lower edge of the chevron spines are unfinished in both. This edge has very little of the convexity which is so marked nearly all along the series in B. musculus, giving them the semicircular form in the latter. The 2nd alone in Megaptera shows much convexity, the 3rd and 7th a little; the 4th is, on the whole, the best developed of the chevron spines. In the subjoined table of measurements of the chevron bones of Megaptera, the 4th of B. musculus is given for comparison.

Individual Chevron Bones.—The *first* presents two separate triangular laminæ, 3½ inches in height, about 3 inches broad at the top, the point directed downwards and forwards. The *ninth* is smaller than the 1st, its more blunt point directed straight down. The laminæ of the *tenth* are oval, 1¼ inch in height, 1¾ antero-posteriorly. Their articular surface, however, is very distinctly marked above, and reaches some way down on the inner side, very sharply marked off from the smooth oval internal surface

proper. The *seventh* shows exceptional narrowness of the articular surfaces (breadth, 1¼ inch; breadth of sixth, 2 inches; of eighth, 1¾ inch), with consequent thinning of the laminæ and much greater width of the arch than in the sixth. This is the chevron bone belonging to the first vertebra, in which the anterior and posterior hæmal tubercles meet to form a continuous ridge.

[The corresponding chevron bone in *B. musculus* (the 12th) is that on which the articular surface begins to diminish to a marked extent in breadth, but the narrowness is continued on the chevron behind it.]

41. TABLE VIII.—*Measurements of the Chevron Bones of Megaptera, and of the 4th Chevron Bone of B. musculus, in inches.*

	Megaptera.										B. musc.
	1	2	3	4	5	6	7	8	9	10	4th
Height of the arch, . .	..	3	3	3	2¾	2⅝	2¼	1⅞	...	...	4½
Width of arch at top, . .	...	1¼	1	1	1	1	1¾	1	...	...	3⅛
,, ,, at the middle,	...	1⅞	1⅝	1⅝	1⅛	1½	2	1½	...	...	2½
Breadth of lamina at top,	3⅛	4⅜	5	5	5	4½	4⅜	3½	2¾	1¾	4⅛
,, ,, at junction	...	3	3¾	3⅞	4	3¾	3⅞	3	...	...	3½
Breadth of spine (ant.-post.),	..	3⅛	5	5½	5⅛	4	4⅛	3	...	...	5½
Height of spine, . . .	...	3⅜	3½	3	2⅛	2	2¼	1¼	...	...	5¼
Height of entire bone, .	3½	7	7	6½	5¾	5⅝	5	3⅞	2⅝	1¼	10

42. EXPLANATION OF PLATE VI.

Fig. 17. Posterior aspect of atlas of Megaptera longimana, reduced to ⅛. *a*, *a*, the lateral articular surfaces; *b*, mesial articular surface; *c*, ligamentous area. The form of the spinal canal, its neural and odontoid parts, is seen. Compare with this figure the figure showing the same aspect of the atlas of B. musculus, with the transverse ligament, in this *Journal*, vol. vii., 1872, fig. 5. In Megaptera observe especially the quadrate form of the ligamentous area, and the presence of a mesial articular surface separating the lateral articular surfaces below. The difference between the right and left shallow groove between the lateral and mesial articular surfaces is seen in the figure. The small surface seen below the mesial articular surface, on the subaxial peak of the atlas, is not articular. The very slight projection of the lateral articular surfaces at the transverse processes is seen in the figure.

Fig. 18. Sternum and first pair of ribs of Megaptera longimana, seen from before, reduced to $\frac{1}{12}$. *a*, *a*, the rough part on the inner border of the rib near the wing of the sternum; *b*, *b'*, anterior angle of right and left rib, less developed on the left; *c*, *c'*, posterior angle of the ribs. The left rib is seen to be shorter than the right. The notch between the two angles here is seen to be shallower on the left rib.

Sternum.—The dotted part on the cervical process is where it has been covered by cartilage. The sub-cartilaginous end of the wings is not seen when viewed from before. The figure shows the more horizontal direction of the posterior border of the right wing, in adaptation to the greater projection of the anterior angle of the right rib. On the left side, the hollow between the wing and the cervical process is seen to be more filled up than on the right side, but the difference on the two sides is not so great as that between the wing and the posterior process. The radiating lines indicate the direction of the vascular grooves and foramina, converging to the thicker part of the bone.

Compare with this figure the figure of the corresponding parts in B. musculus, in this *Journal*, vol. vi., 1871, fig. 4, showing the ligaments of the two costo-sternal articulations, &c.

(*To be continued.*)

Notice of Book.

The Anatomie of the Bodie of Man. By Thomas Vicary. Edited by F. J. Furnivall, M.A., Dr Phil., and Percy Furnivall, Student of St Bartholomew's Hospital. London, 1888.

THOMAS VICARY was in his day a man of note amongst surgeons. Born about the end of the 15th century, he became in 1530 Master of the Barber-Surgeon's Company, and was in succession surgeon to Henry VIII., Edward VI., Mary, and Elizabeth. After the foundation of St Bartholomew's Hospital was handed over by Henry VIII. to the City of London, Vicary was made chief surgeon to the Hospital, which appointment he held till his death in 1561 or 1562. In 1548 he published his *Anatomie*, which is the first book published in English descriptive of the anatomy of the human body, and a reprint of this book was issued by the surgeons of St Bartholomew's in 1577.

An edition of this reprint has been prepared by the Messrs Furnivall for the Early English Text Society, along with a Life of Vicary, Notes on Surgeons in England, St Bartholomew's Hospital and London in Tudor Times, and an Appendix of documents and illustrations. The book contains a quantity of most curious and valuable information bearing on the history of the medical profession in London in Tudor times, which has been gathered from a variety of sources, and edited with great care. It will be read with pleasure by all who take an interest in the rise of the medical profession in this country. What, however, more especially concerns the readers of this *Journal* is the treatise on anatomy. Vicary, like Harvey, was a man of Kent, and they were both officers of St Bartholomew's Hospital. If any one will compare Vicary's chapter on the heart with the account given of that organ in the immortal tractate *De motu cordis et sanguinis*, published in 1628, they will see how infinitely in advance Harvey was in his knowledge of the anatomy and physiology of that important organ, and will be able to realise how, without this advance, physiology and medicine must have remained fields productive of nothing but visionary hypothesis and barren conjecture.

Journ. of Anat. & Phys., Oct.r 1888.

Vol. XXIII } Pl. I
N. S. Vol. III }

Fig. 1.

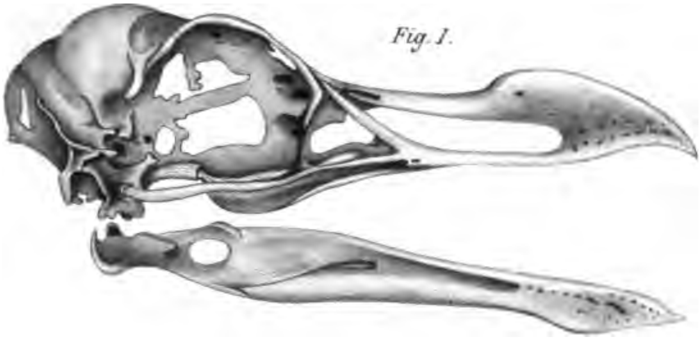

Fig. 2.

Fig. 3.

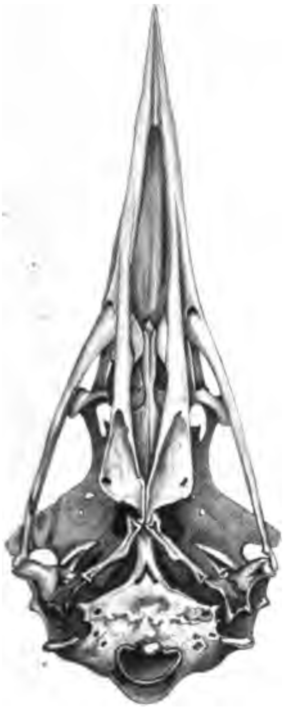

Fig. 4.

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ARCTIC & SUBARCTIC WATER BIRDS.

Journ. of Anat. & Phys, Octr 1888.

Vol. XXIII / N. S. Vol. III } Pl. II.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

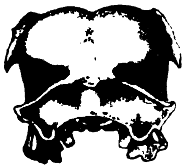

Fig. 13.

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ARCTIC & SUBARCTIC WATER BIRDS.

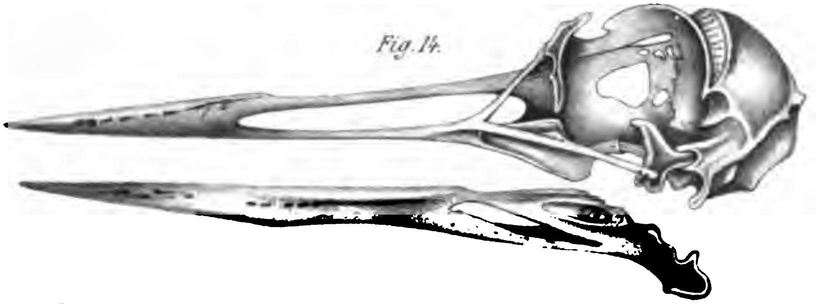

Fig. 14.

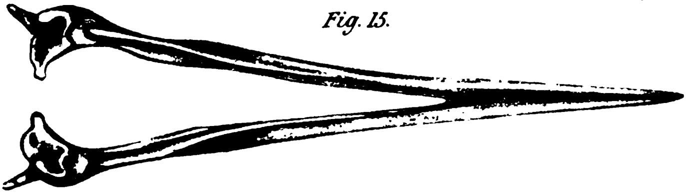

Fig. 15.

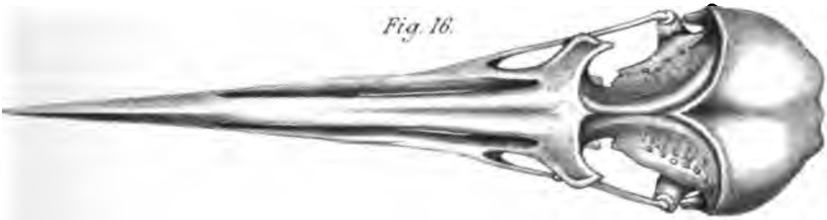

Fig. 16.

Fig. 17.

Fig. 18.

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ARCTIC & SUBARCTIC WATER BIRDS.

Journ. of Anat. & Phys., Octr 1888.

Vol. XXIII / N. S. Vol. III } Pl. IV.

Fig. 19.

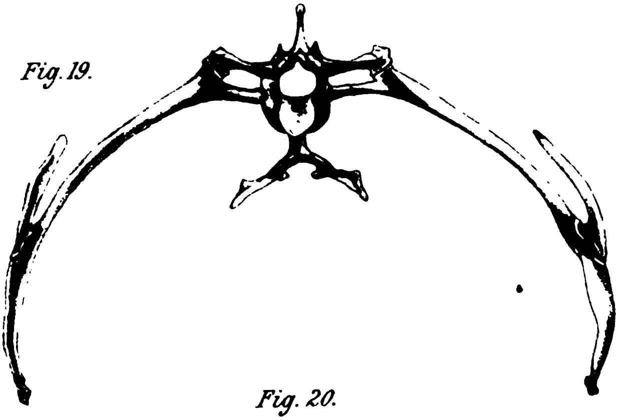


Fig. 20.

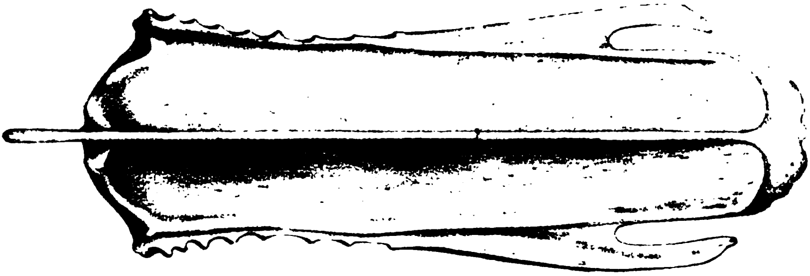


Fig. 21.

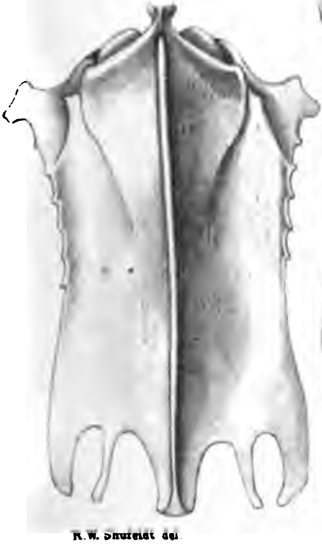
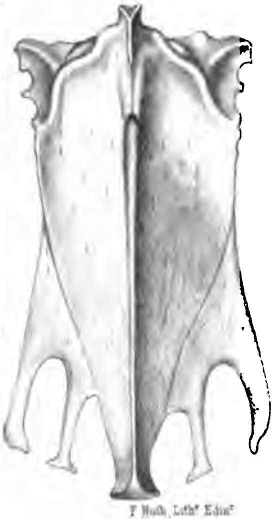


Fig. 22.

Fig. 23.



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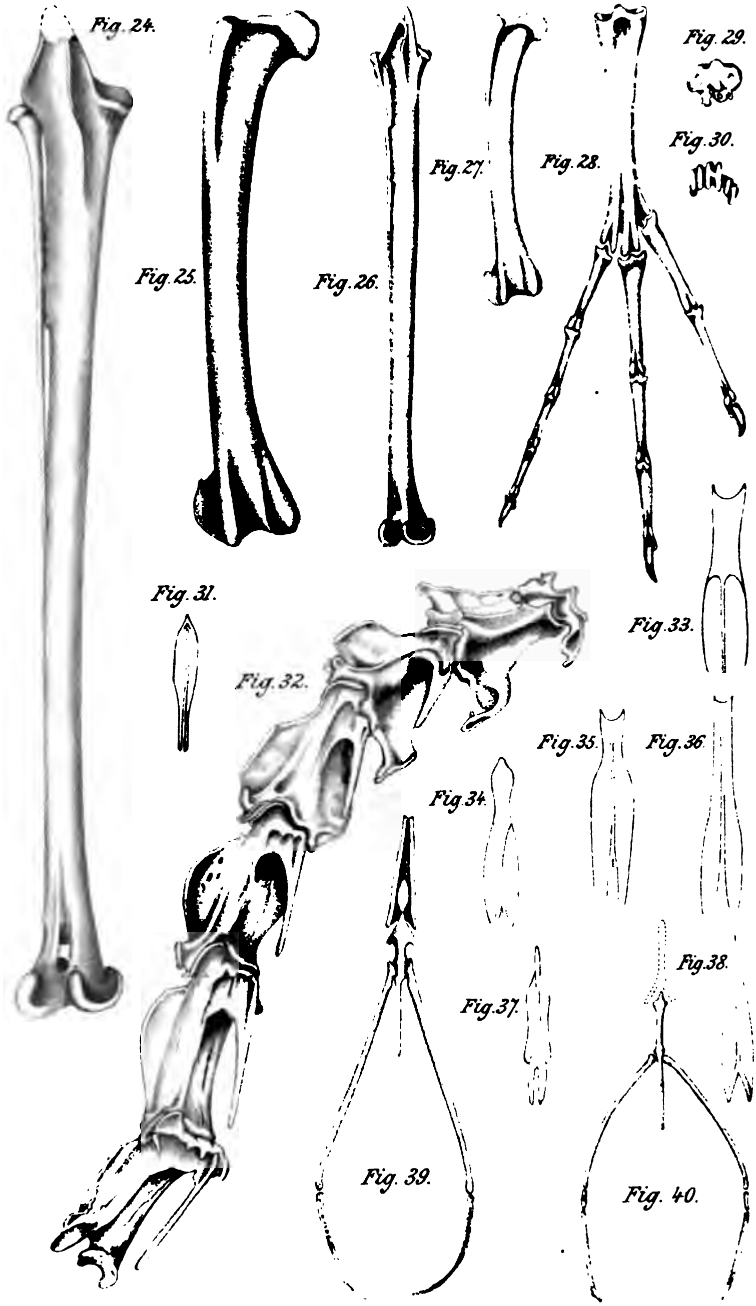
ARCTIC & SUBARCTIC WATER BIRDS.

Journ. of Anat. & Phys., Oct.r 1888.

Vol. XXIII
N.S. Vol. III } Pl. V.



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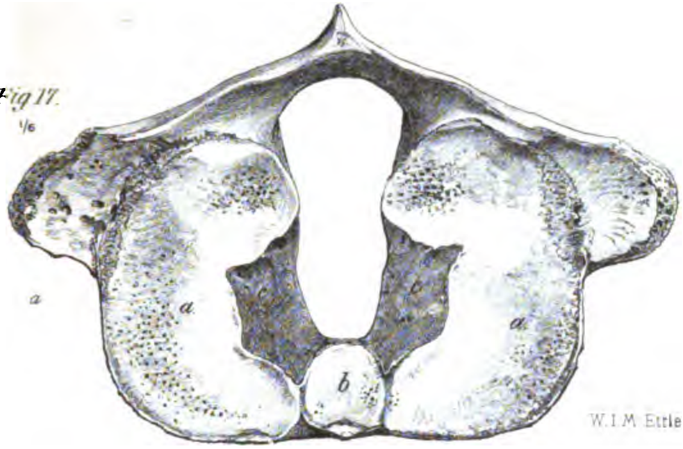

FIG. 17. Atlas of Megaptera Longimana, hinder aspect.
a. a. Lateral articular surfaces.
b. Mesial articular surface.
c. c. Ligamentous Area.

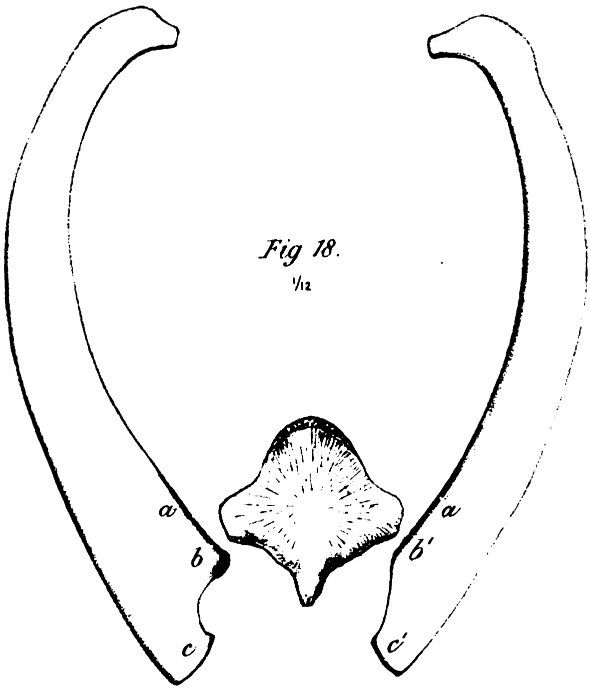

FIG 18. Sternum and First Pair of Ribs, anterior aspect.
a.a. Rough Part of costal border.
b. Anterior, and *c.* Posterior angle of end of Right Rib
b' and *c'* Same parts of Left Rib showing the differences.

John Struthers Delt

MEGAPTERA LONGIMANA.

Andw. Gibb & Co. Lithrs. 3 Queen St. Abdn.

Journal of Anatomy and Physiology.

CONTRIBUTIONS TO THE COMPARATIVE OSTEOLOGY OF ARCTIC AND SUB-ARCTIC WATER-BIRDS. PART II. By R. W. SHUFELDT, M.D., C.M.Z.S. (PLATES VII., VIII., IX., X., XI.)

(*Continued from page* 39.)

IN the present Part it is my intention to give a comparative account of another genus of the family *Alcidæ*, and compare the data with the description of the skeleton of *Alca torda*, already published in Part I. (p. 1, Vol. III. N.S.).

We will now take up the osteology of the genus *Uria*, of the subfamily *Alcinæ*, and the material at my hands for this purpose is given in the subjoined table, although, in addition to the specimens there enumerated, I have by me a quantity of odds and ends of skeletons of more or less nearly related forms, which will greatly assist me in many points where an explanation of certain osteological characters is demanded.

With the full description of such a type as *Alca torda* before us, and with a similar description, made comparative, of such a bird as *Uria troile* at our command, we shall be in an admirable position to fully discuss in subsequent parts of this work all the other genera of *Alcidæ* and their kin. This it is my intention to do; and for the purpose I have at hand some 150 skeletons of the Order in question.

Now, although this material will not admit of a very exhaustive comparison of the skeletons of all the species and subspecies of this genus *Uria*, yet I think, beyond doubt, we can at least arrive at a full description of the osteological characters of the interesting group of birds contained in it.

Tabulated List of Material.

Specimen and Sex.	Condition, &c.	Complete or Incomplete.	Source.	In whose possession at present.
Uria troile californica.	Skeleton in the rough.	Complete, No. 16,973, Smithsonian Collection.	Farallone Islands, C. H. Townsend, collector.	Smithsonian Institution, Washington, D.C.
Uria troile californica.	Ditto.	Do., No. 16,974.	Ditto.	
Uria lomvia arra, ♀.	Sternum and shoulder girdle.	Complete, No. 16,795, Smithsonian Collection.	Lieut. P. H. Ray, collector, Point Barrow, Alaska.	
Uria lomvia.	In the rough.	Limbs, hyoid, and small bones missing, No. 16,783, Smithsonian Collection.	Collector unknown, Upernavik, Aug. 15, 1883.	
Uria troile, ♂.	Sternum and pectoral arch.	Complete, No. 16,986, Smithsonian Collection.	N. P. Scudder, Davis' Strait, July 12, 1879.	
Uria troile.	Ditto.	No. 16,985, Smithsonian Collection.	Ditto.	
Uria (sp. ?).	Bleached skull, beach specimen.	Incomplete, No. 17,009, Smithsonian Collection.	W. H. Dall, collector, Unalashka.	
Uria (sp. ?).	Sternum, ditto.	Incomplete, No. 17,008, Smithsonian Collection.	Ditto.	
Uria (sp. ?).	Skeleton in the rough.	Skull and other parts missing.	Ditto, Plover Bay.	

Of the Skull.

Figures of the Murres are presented in Plate VII. figs. 1–4 inclusive, with their descriptions given under the Explanation of Plates. With the skulls of *Alca torda* and any of the species of the genus *Uria* before one, a glance is sufficient to satisfy the osteologist that they are from birds which represent closely related groups, and a more careful examination of these skulls soon convinces one that in many of their characters they are very much alike indeed.

In *Uria t. californica* the superior mandible is long and gradually tapers to its apex, the culmen, being nearly flat behind to almost imperceptibility, become roundly convex to the tip.

Brünnich's Murre has a similar superior mandible, only it is somewhat broader behind and not nearly as long, consequently tapers more rapidly to its apex. Both these forms differ from *Alca* in this respect, in not having the mandible hooked at the end, with its anterior half compressed and convexly raised above the posterior half of the culmen in the median line.

All have large, pervious, sub-elliptical, external osseous nares, without a vestige of a bony septum; all are likewise schizorhinal birds. An individual difference here takes place, sometimes in the form of the slit in the nasal bone. Specimen No. 16,974 has the two cornua of the nasal bone of either side nearly in contact along their posterior halves. This seems to be due to a depressed condition of the cranio-facial region in this particular individual, for in all the other specimens the slit is carried clear back, and the cornua do not come in contact. Upon lateral view of these skulls of *Uria* I am inclined to think, after careful examination, that the "os uncinatum," as I described it for *Alca torda*, may be absent or aborted, or if it does exist, as in the last mentioned Auk, is very much smaller. The *lacrymal* bears the same relation to the ethmoidal wing, being anchylosed more or less firmly to its outer margin, thus forming in *Uria* as in the Razor-bill quite a complete partition between the orbit and rhinal chamber.

Both these genera have the raised rim on the circularly arched and superior periphery to the orbit, with the vault of that cavity slightly elevated from the median septum outwards. So far as I am able to judge from the material in hand, I find, too, that the deficiencies in the true osseous orbital septum are greater in *Uria* than they are in *Alca*. Exactly how this is may be better seen by a comparison of the skulls in the figures. Of all the specimens before me, the foramen opticum in *Uria* always merges with the large vacuity in the septum. This does not take place in either of my skulls of *Alca*. A comparison of the hinder halves of these skulls, from a lateral aspect, goes to show that the differences among them are very insignificant, and mainly depend upon individual departures from the ideal type. The bulging upwards of the supraoccipital protuberance seen in the Murre, falls within this category of departures, as a difference existing between this particular skull and the one I have

chosen to figure of *Alca*. As a constant character, however, the crotaphyte fossa seems to be deeper and wider in the Razor-bill than it is in Brünnich's Murre, and no doubt largely in consequence, its posterior wall is found to be higher and more prominent. The difference among the quadrate bones of the various species of the two genera are of so slight a nature as hardly to be appreciable.

Comparing these skulls from a *superior view*, we again find the form of the anterior half of the mandible to be the only evident difference among them; and indeed, were it not for this, it would be hard to distinguish the skulls from each other, relying solely upon the appearance of the upper aspects of their hinder halves.

In all, the supraorbital glandular depressions are practically alike, and agree with *Alca*. The antero-external foramina of these fossæ are present in all, having the same general form in each species. In the particular specimen of the skull of Brünnich's Murre before me, these glandular depressions seem to be deeper and the posterior foramina more numerous and longer. They are here, too, simply separated by a thin median crest of bone.

In both genera there is a more or less perfect bony partition thrown across from the vault of the skull to the inner aspect of the orbital periphery, dividing either supraorbital glandular depression from the extreme anterior part of the crotaphyte fossa of the same side.

Alca, it will be remembered, had in the median line behind, on this aspect of the skull, a narrow isthmus of bone dividing the inner rounded terminations of the crotaphyte fossæ. In both my specimens of this Auk, this isthmus is 1½ millimetres wide at its narrowest part. Now this same division is seen between these fossæ in *Uria*, but in the two adult skulls collected by Mr. Townsend in the Farallone Islands, I find that in specimen No. 16,973 this isthmus measures transversely, as we measured it in the Razor-bill, 4 millimetres, whereas in specimen 16,973 it measures 7 millimetres, or is nearly double the width in the last specimen.

In the specimen of Brünnich's Guillemot it is about 6 millimetres wide. This is but another instance of the care we must

exercise in our judging of such differences and the weight we attach to them. A variation of this kind is nothing more than we are very apt to find in a good series of skulls of any vertebrate form, and depends altogether upon the constitution of the particular individual possessing it. Who, for instance, has not been struck by the extraordinary differences that are to be found in a series of female human pelves. One pelvis will be found contracted, with perhaps, among a list of other differences, very thick walls to the iliac fossa, where another will be observed that is broad and capacious, with the wall of an iliac fossa so thin that, as I have seen, a large vacuity may actually exist in it.

Such an example as this applies with special force to the skulls of our Murres, for to return to them we find upon direct posterior aspect, that in the specimen of *Uria t. californica*, No. 16,973, there is on either side of the median line a very large, subelliptical supraoccipital foramen, of which there is no trace of such a thing in No. 16,974 of the same species. Taken in connection with the narrower isthmus dividing the crotaphyte fossæ, which may also be seen upon this view of the skull, and other minor differences that result as a consequence of this configuration, the skulls of these two specimens, from this view, have indeed a very different appearance.

I have no doubt whatever, though, that if a selected series of say fifty were taken, that all the intermediate styles could be found. This is nothing more than a glimpse of the general law of the intergradation of all forms, and the instability of species.

Still more alike are the basal aspects of the skulls of these two genera, for from this view the difference in form of the bill of *Alca* passes out of sight.

In comparing the points that present themselves upon this side, even in genera more widely separated from each other than *Uria* and *Alca* are, Professor Huxley, in his *Classification of Birds* found it very convenient to figure the basal views of the skulls of *Alca torda* and *Larus rissa* side by side, for the purpose of comparing the slight differences that existed between them, and better to show the underlying fundamental principle upon which both of these types were built. Moreover, this profound anatomist is compelled to admit, in the memoir in question, that—

"The osteological resemblances between a Plover, a Gull, an Auk, and a Diver are so close that it is utterly out of the question to regard these birds as members of different orders."

We find in *Uria*, as in *Alca*, that the abutment of the ethmoid beneath the proximal end of the nasal process of the premaxillary is transversely divided about in line with the cranio-facial hinge. The union is very slight, and in a beautifully beach-bleached specimen of a skull of a *Uria*, collected by Dall at Unalashka, this anterior triangular piece is broken off, and shows very well how slight this connection was with the remainder of the bone.

In the various species of *Uria* the *maxillo-palatines* are essentially the same as I described them for the Razor-bill; they are, on the whole, however, comparatively smaller, and considerably further apart.

I described the *vomer* of *Alca* as anchylosing with the ascending processes of the palatines. This is not the case with the vomer in the Murres, as the sutures between these bones are ununited, although the surfaces are continuous and alike in both. It may be that my specimen of *Alca* is a very old bird, and in younger specimens, or specimens of the same age as these Murres, they would be like them in this particular. Probably this is the case. The form of the palatines and pterygoids, the shape and character of the rostrum, and the mode of articulation of all these, is practically alike in both genera.

Within the brain case of the Murre I find the bony ridges on the vault that mark the divisions of the cerebral lobes rather feebly developed, while the elevations, prominent and subcircular, that define the location of the semicircular canals of the ear are very conspicuous. The pituitary fossa is deep, with high posterior wall, that shows a median perforation, and the openings at its base for the internal carotid arteries are thoroughly individualised.

In addition to its greater length, I find the rami of the *mandible* of the Murre shallower than they are in *Alca*, with the symphysial end far more obliquely truncated. The elliptical vacuity in the surangular holds the same position as in the Auk; it is very large in the specimen of Brünnich's Murre. The articular ends are constructed very much alike, and the

facets are the same in number and arrangement. We also find the recurved processes at the angles in *Uria*. Specimens of the Murre of the Pacific coast show no pneumatic foramina in their mandible, and I doubt very much that air ever finds access to the cavities of this bone in these birds, most certainly only to a limited extent in the Auks.

Brünnich's Murre has its *hyoid arches* constructed very much as we find them in the *Laridæ*. The glosso-hyal is all in cartilage, while the cerato-hyals are the only elements of that part of the apparatus which ossifies, and their transverse band of union is also a cartilage for the articulation of the anterior end of the first basi-branchial. This latter anchyloses with the second basi-branchial, which is comparatively short and spiculaform. The cerato-branchials and epi-branchials articulate as usual, and curve up behind the cranium as in most birds.

Of the Vertebral Column of the Genus Uria.—We find in *Uria troile californica* that the anterior cup of the *atlas* is perforated by a circular aperture at its superior periphery. Its postero-superior and inferior angles have backward directed processes, the upper ones being on the neural arch, and the lower ones on the centrum.

In the *axis* the odontoid process is flat above and convex beneath. When articulated its apex is in the perforation of the cup of the atlas behind, and its lower surface rests in a concavity intended for its reception, posterior to it.

A prominent neural spine projects backwards from the hinder aspect of this vertebra, and the postzygapophyses on either side have the same direction and are much elevated. Their facets, however, looking almost directly downwards, are at their inferior basis. Posteriorly, beneath the centrum, the axis also develops a strong quadrate hyapophysis, the inferior margin of which is thickened.

Many of the characters of the second vertebra are still to be found in the third; the neural spine, the elevated postzygapophyses and the hypapophysis are all present. It has in addition, however, the lateral canals; parapophysial spines directed backwards; elliptical and sessile prezygapophysial facets, which are partially yoked with the posterior processes by intervening bone, that usually shows a small perforation

on either side. In most respects the fourth vertebra is like the third, the lamina of bone and its perforations still being retained between the pre- and post- zygapophyses; it will be remembered that it was reduced to the finest imaginable connecting bar in *Alca* in this vertebra.

The neural spine of this fourth vertebra has been moved more to the centre of the bone, while the elevated processes above the postzygapophysial facets are shorter, thicker, and more transverse in this direction, the facets themselves being considerably larger.

In the *fifth vertebra* the lateral canals are of a larger calibre; the hypapophysis is longer, while the stumpy and short neural spine is in the middle of the bone. Still more important are the changes in the postzygapophyses—these now have the oblong facets occupying their extreme ends, the processes themselves being equally directed outwards and backwards, with metapophysial markings on their superior aspects.

The articulations among the centra of these vertebræ in the cervical region of the column are of the heterocœlous type.

In the *sixth, seventh, eighth,* and *ninth vertebræ,* the neural spines and hypapophyses have disappeared, and the parial parapophyses become from the sixth to the ninth inclusive progressively shorter.

A lateral canal in the first of this series of segments is nearly circular, and of a size not much smaller than the similarly formed neural canal. The latter gradually increases in size as we go backwards, while the former diminishes. It is also these four vertebræ that alone form the open channel for the protection of the carotids.

Characters peculiar to themselves are also seen in the *tenth, eleventh, twelfth,* and *thirteenth vertebræ.*

The neural spines are still absent, though the slight appearance of one is evident in the last of this series; the prezygapophysial facets are long and elliptical, directed upwards and inwards; the postzygapophyses become progressively shorter and thicker; the neural canal becomes slowly rather larger and nearer an elliptical outline transversely. A large median quadrate hypapophysis is on the tenth vertebra, it also becomes gradually smaller to disappear almost altogether on the thirteenth, where it is represented by a low, median crest.

The processes that so largely help to form the outer walls of the lateral canals, in each vertebra as we proceed towards the dorsal column, are shaping themselves more and more like the primitive rib, or pair of ribs rather, that they eventually will result in.

These make their appearance in the *fourteenth vertebra,* the same one in which they do in *Alca.* This segment in *Uria,* of the vertebral column, has also other characters worthy of our investigation. A long, posteriorly forked neural spine has appeared once more; diapophyses, broad and with rounded outer extremities, are thrown out laterally, while the postzygapophyses are now quite short. The neural canal is large and transversely elliptical. Projecting from the sides of the centrum beneath, there is a thin lamina of bone, directed downwards and outwards; it is the beginning of what afterwards becomes so highly a developed hypapophysis in the vertebræ of the dorsal region.

In the *fifteenth vertebra* the neural spine is a quadrate longitudinal plate of bone, as it is in the remainder of the series to the sacrum; the neural canal is contracting in the size of its calibre; the sides of the centrum are pitted, but those, as in the other vertebræ of this Murre, are non-pneumatic. The quadrilateral hypapophysial plates, though directed as in the last vertebra, have here approached each other, so as to have a common sessile base in the median line. The large articular ends of the centrum are nearly square in outline, the anterior one being convex from above downwards, concave from side to side, the reverse condition obtaining with the hinder facet. This vertebra supports a long pair of free ribs, which in this specimen had anchylosed unciform appendages of considerable size. They are articulated on the other ribs behind, being long and slender, as we found them in *Alca torda.*

Vertebræ of the dorsal region in *Uria* possess characters which are also peculiar to themselves. Chief among these is the change that takes place in the articulations among the centra. This commences with the posterior facet of the sixteenth vertebra, which shows a very faint inclination to become concave. In the middle of the series, however, and thence backwards to the sacrum, the facets of the anterior ends of the centra are

hemiglobular in form, which are received into corresponding concavities at the hinder aspects of each centrum preceding. Owen found the same thing during his examination of the skeletons of Penguins and Auks, and says "the posterior surface of the second or third dorsal vertebra is concave, to which the opposed end of the succeeding vertebra presents a corresponding convexity: the 'opisthocœlian' ball-and-socket joint is continued between the centrums to the last dorsal." I would remind the reader in this connection that the extinct toothed *Ichthyornis* of the Cretaceous beds of this country had amphicœlous vertebræ, such as obtain in fishes.

The *sixteenth vertebra* is connected with the sternum by its ribs descending to meet costal ribs. Its hypapophysis is still bicornuted, with the pedicle a little more pronounced. This character of the dorsal vertebra is a very striking one, for in the succeeding vertebra the pedicle is very long, and the cornua wide and spreading; longer still in the next, the cornua are contracted and directed forwards. From this on to the last free vertebra before arriving at the sacrum, the pedicles become shorter again, being laterally compressed, thin plates, with antero-posteriorly dilated extremities, the fore and hind ends of which nearly touch each other, and in life are connected by a ligament.

In these vertebræ, too, the centra are much compressed from side to side except at their articular ends. The transverse processes stand directly out from their sides, and, together with the neural spines, they are confined somewhat by an interlacement of long, bony spiculæ. Some of these project also from the anterior part of the sacrum. These vertebræ all have *ribs*, of the same style as those I described for *Alca*, connected with the sternum through hæmapophyses. As in all true Auks, they sweep far behind in graceful curves, stamping the skeleton of this group of birds with a peculiar character possessed by no other. Agreeing with *Alca*, we find in *Uria* that the *twenty-second vertebra* is the last free one of the dorsal region, and its ribs connect with the sternum by very long delicate sternal ribs.

The ribs of the sacrum of these two genera differ, however, for in *Alca* both pair articulate with the vertebræ beneath the ilia, the hæmapophyses of the anterior pair reaching the sternum

to articulate with the eighth and last pair of facets on the costal borders of that bone. The hæmapophyses of the last pair of ribs are long, but do not reach the sternum. Now, in *Uria* the anterior pair of ribs beneath the ilia articulating with the first vertebra that anchyloses with the sacrum have hæmapophyses that do *not* reach the sternum; the last pair neither reaches the sacrum nor the sternum, both costal and vertebral pair being "floating ribs." Of a consequence, we find in *Alca* eight facets for hæmapophyses on a costal border of the sternum, whereas *Uria* has but seven—a number which I have verified from all the material at my command.

Of the Pelvis and Coccygeal Vertebræ.—My tabulated list of material shows that I have four pelves of specimens of the genus *Uria* to examine—the two Murres from the Farallone Islands, an unidentified specimen, probably *U. troile*, and the pelvis of Brünnich's Murre. This latter will be figured in a subsequent part of this series, shown upon superior aspect, and may be conveniently compared with the same view of the pelvis of the Razor-bill in the plate.

Notwithstanding the differences that are to be found among the pelves of the same species, as exhibited by the four examples of this bone before me, the fact still remains evident that these two genera of birds are closely allied to each other, so far at least as this part of the skeleton can teach us.

In *Uria t. californica*, as in *Alca*, it is still long and narrow, with the post-pubis drawn out behind, as well as the ischium and, to a much less extent, the ilium. The triangular notch is present between the two latter bones on this border. Viewed from above, we find that the antero-internal borders of the ilia come in contact with the crest of the front part of the neural spine of the sacrum for some little distance, thus converting the "ilioneural grooves" in this locality of the Razor-bill into "ilioneural canals" in the present genus.

The extent to which this is carried differs in individuals of the same species. Next we note that in the pelvis of *Uria* there has been a gain on the part of the post-acetabular area, whereas the pre-acetabular superficies is about the same in amount in the two genera. This seems to have been brought about by a widening of the pelvis behind in the Murre. Owing

to the spreading of the ilia anteriorly, Brünnich's Murre has this balance re-established, although in this bird the pelvis is in general wider and shorter than it is in *Alca*. It also has the ilioneural grooves instead of canals. The figure of the pelvis in Brünnich's Murre shows, too, that the ilia may become perforated, due to incomplete ossification in its thin anterior parts.

Upon lateral aspect the pelvis of *Uria* deviates but very slightly from the Razor-bill Auk. It has spread out rather in its hinder half, simply changing the perspective of the parts a little on this view, but very little, and an amount that would hardly be appreciable at the first glance.

Let us now look at the inferior sides of these four pelves. We found fourteen vertebræ in the sacrum of *Alca*; of these in *Uria* there may be thirteen or fourteen, and the difference seems to be due to the fact as to whether the inner borders of the ilia grasp an additional one behind or not, or whether it remains free as an extra caudal one. Such a variation may take place among any of the vertebrates. The rule seems to be, for both genera, that the first five anterior vertebræ of the sacrum throw out their transverse processes as abutments against the under side of the iliac bones. One of the specimens of the Murres even forms an exception to this (No. 16,973 of tab. list), for in it I see the sixth vertebra also throws out its processes in a similar manner on the very verge of the pelvic basin proper. Here we have it again how birds, even of the same species, may vary in such a character as this. Very marked differences are seen in this particular specimen in the anterior vertebra of the sacrum. Its centrum, although anchylosed as in the other specimen of the same species, shows the line of anchylosis so distinctly that the vertebra almost looks as if it might be detached. Its transverse processes, however, are thrown up against the iliac walls, and articulate with the anterior pair of sacral ribs. The post-pubis has in Brünnich's Murre a longitudinal groove running nearly the whole length of its outer side, most plainly marked near the middle of its course. How constant this may be I am unable to state.

So, after all, the best we can say for the differences in the pelves of these two genera, is, there seems to be a gain on the part of the postacetabular area over the preacetabular, and

something of a widening of the bone posteriorly. As apparently insignificant as this difference is, it must be borne in mind, as several of these groups grade insensibly into each other, and such a fact may have its weight further on, when the other forms are taken up. Normally, the number of coccygeal or rather *caudal vertebræ* is eight, with at least four or five more in the long and completely co-ossified pygostyle. Sometimes the anterior one may be appropriated by the sacrum. In *Uria* their form and general character agrees with the bones, as I found and described them for *Alca*. More or fewer of the hinder ones show the chevron bones also freely articulated, as in the skeleton of the tail of the last-mentioned Auk.

Of the Pectoral Arch.—The shoulder girdles of the different species of *Uria* resemble each other very closely, and depart but very little from the arch as it exists in *Alca*. We still find the long head to the clavicle, with the articular raised facet near the middle on the outer aspect for the head of the coracoid. Its arch, both from front and side view, is practically the same, it being a perfect type of the U-shape on the former, and it is seen to curve backwards on the latter, so that its lower part just clears the upper edges of the prominent carinal angle, or better, what in these birds is really a carinal prominence. In the coracoids we find that their heads overlap the above-mentioned facet intended for them on the outer side of each limb of the furcula, in the same peculiar manner as they do in the Razor-bill. The scapular process of a coracoid is also here perforated by a foramen that is constant. Brünnich's Murre has the anterior aspect of the lower part of the shaft strongly marked by muscular lines. The articular base for the sternum is, comparatively speaking, not as thick through antero-posteriorly as in *A. torda*.

The process which projects so prominently from the lower and outer margin of the coracoid is hooked upwards in *Uria*. Each *scapula* is long, narrow, and moderately arched. Behind it is truncate with rounded tip, while anteriorly its head is compressed from above downwards, and occupies the entire superior line of the scapular process of the coracoid. The posterior tip of the clavicle fails to reach either of these parts in any of the forms thus far examined.

All the bones composing the pectoral arch of the genus *Uria* are non-pneumatic.

Of the Sternum of the Murres.—From all that has been said above, we could hardly expect to find any great difference in the sternum between the two genera of Auks thus far examined, nor is there any. The same general pattern stamps them both, and perhaps a study of the figures I present, and in which I have aimed to give the greatest accuracy on this account, will give us a better idea of the deviation in form than any written description can do, however exhaustive in detail.

A lateral aspect of the sternum of any *Uria* shows the same general outline of the bone as we saw it in *A. torda;* the same plan of keel and body; the same prominent carinal angle, and the wedge-shape manubrium. If it prove to be constant, perhaps one of the best distinctions is the number of hæmapophysial facets on the costal border; in eight sterna of Urian species there are seven of these against eight on the only sternum I have of *Alca torda.* On the lower aspect of the bone the muscular lines take the same course practically as we found them in the Razor-bill; in *Uria,* however, the sternum here is generally wider, with its xiphoidal end much more broadly rounded.

The notches on the whole I expect will not be found to be as large in proportion in *Uria* as they are in *Alca,* but these will be of little use or help in the way of generic distinction, as in some specimens of Murres they are larger upon one side than they are upon another, and in one specimen collected by Mr N. P. Scudder (No. 16,986) for the Smithsonian Institution at Davis' Straits, the *foramen* on one side is exceedingly small, while no sign whatever exists of either foramen or notch on the other. It may be that a series of sterna of *A. torda* would show a like assemblage of eccentricities. I had something to say to the same effect upon this point in my "Osteology of the *Carthartidæ,*" where a number of instances were presented showing the variation that may exist in this condition. For it seems to depend entirely upon the way in which any individual sternum may complete its xiphoidal end by ossification; that is for the same species. Of course, no such caper could be cut by any such sternum as possessed by the *Gallinæ* or like forms,

nor could the fundamental principle, whatever it may be, that has produced a now-existing group of birds with a four-notched sternum, and another with a two-notched one, be changed, whatever freaks may take place in the modifications of either.

I find in the two sterna collected by Mr Scudder that the clavicular arch is much further removed from the upper edge of the carinal prominence than I described it to be above. This may be a difference between *U. troile* and *U. arra.*

In *Uria* the sternum shows scarcely any concavity behind on its upper side, in some specimens being quite flat. Others show the mesial ends of the coracoidal grooves meeting behind the manubrium, while in some specimens quite an interval exists there. They meet in my specimen of *Alca.* In both, generally, the sternum is a thoroughly non-pneumatic bone, not even the traces of rudimentary apertures for such purposes existing in any of the usual sites when they occur in others of the class.

Of the Pectoral Limb.—Murres, in common with the Razor-bill Auks, have non-pneumatic bones in the skeletons of their wings, and in their preparation in the rough, as collectors bring them in from the field, we find the bones all very dark and saturated with the oils that have oozed through from the small medullary cavities within.

In *Uria troile californica* I find the humerus has a length of 8·85 cm.; the ulna, 6·9 cm.; the radius, 6·6 cm.; carpo-metacarpus, 4·5 cm.; pollex phanlanx, 1·9 cm.; proximal phalanx of index digit, 2·0 cm.; its distal one, 2·35 cm.; and the single small phalanx of middle digit, 0·9 mm. This constitutes a very well proportioned wing, and its owner is a good flyer.

The general character of the bones of the pectoral limb in *Uria* agrees with the corresponding limb bones of *Alca torda.* Except for the difference in size it would be difficult indeed to put one's finger upon a single point of marked dissimilarity between them.

The proximal end of the *humerus* has the jutting end of the ulnar crest, with its deep pseudo-pneumatic fossa. The radial crest is low and carried down as a line upon a shaft that is flattened quite as much in proportion, and in the same manner as we found it in the Razor-bill.

In this particular specimen (No. 16,974) the "ectocondyloid process" is but feebly developed, and would hardly attract attention did we not know of its existence in nearly related forms. The ulnar and oblique tubercles are very prominent, large jutting convexities. Otherwise this extremity of the shaft has the same square cut appearance as we saw it in the first Auk described.

Various authors have stated, without any exceptions, that two sesamoids are found at the elbow in Murres; Owen speaks of two such bones in these birds and the Penguins. Coues, in giving his synopsis of characters of the *Alcidæ*, in the second edition of the "Key," is more reserved in his statement, and says "usually (always ?) an anconal sesamoid, sometimes double." Now in this specimen of *Uria* the tendons in which these sesamoids occur have been preserved, and I fail to detect their presence; there is, however, a large, flat, sub-elliptical sesamoid in the fossa on the anconal aspect of this proximal extremity of the ulna. This agrees with the one I have found in the Puffins, and marked *ss″* in fig. 47; the two usually described being the ones marked *s* and *s′* in the same illustration.

The shafts of the *ulna* and *radius* are also flattened as in *Alca torda*, but I hardly think quite as much, proportionately; the papillæ for the quill-butts of the secondaries are not perceptible along the shaft of the former.

This flattening of the ulna gives rise to two surfaces on its shaft contained between two borders—one sharp and distinct, the other rounded. The former extends the entire length of the shaft from the tip of the olecranon to the proximal commencement of the circular margin of the outer side of the distal trochlea of the bone; the latter extends between the base of the cup-like articulation for the ulnar tubercle of humerus to that point at the distal end of ulna that is overlapped by the same extremity of the radius. From this it will be seen that these two borders are upon almost exactly opposite sides of the shaft of the bone.

The method of articulation and the character of the facets and surfaces agree in all essential particulars with the corresponding ones in the Razor-bill Auk.

The shaft of the *radius* is quite straight; it also shows longitudinal borders, one sharp and the other rounded, dividing its two surfaces; but their position is just the reverse from what it is in the ulna. This, of course, brings the *rounded* border of each bone opposite each other and in the interosseous space. When articulated the head of the radius is received into a fossa in the ulna, above which, on the latter bone, there is a wing-like prominence, that on its humeral side has the remainder of the facet for the oblique tubercle.

The distal end of the radius is longitudinally marked by two deep tendinal grooves above.

Uria has the two usual segments in its *carpus*, and they articulate precisely in the same manner as described for *Alca torda*.

In the carpo-metacarpus we also find the rather long pollex metacarpal parallel to and attached by its entire length to the straight and main shaft of this segment of the hand, the index metacarpal.

Its phalanx is a long, sub-trihedral bone without terminal claw or another joint. A rather delicate last metacarpal spans the former from proximal to distal end, and is without any peculiar processes. The lower end of the carpo-metacarpus, on its anterior aspect, has the same process to guide the tendons as we found in the Razor-bill Auk, and as in this bird, too, we find a similar one occupying a like position on the broad proximal phalanx of its digit. Long and sub-trihedral, the ultimate joint of this finger possesses no claw nor rudiment of one.

The joint of the mid-metacarpal is, comparatively speaking, long and tapering; its length is about half the posterior border of the broad joint lying next to it.

From all that has been said above, and with the measurements given before us, it is evident that the manus of this Murre is a very completely developed one, and coincidently adapted to the power of flight possessed by its owner.

Of the Pelvic Limb.—As illustrative of this for the genus, I will take the skeleton of the leg of the same specimen from which our pectoral limb was chosen, and described in the last paragraphs (*U. californica*, No. 16,974). Little is there to be said in regard to it, for, as in several other parts of the skeleton

alluded to, it is stamped with all the characters of the preceding genus, and showing but few inconspicuous departures therefrom.

We note at the outstart that the entire limb is non-pneumatic, there being not the slightest trace of any such foramina in the localities where they occur in other birds.

The femur is 4·6 centimeters long; the tibia, 9·3; the fibula, 6·3; the tarso-metatarsus, 3·8; the proximal joint of inside toe, 1·6; the next of same toe, 1·6; the claw, 0·9. Measuring the middle toe in the same way, we find proximal joint, 1·8; next, 1·5; next, 1·3; its claw, 1·0; the outside toe, proximate joint, 1·5; next, 1·2; next, 1·0; next, 1·1; and the claw, 0·7.

These measurements differ somewhat in different individuals, and in the sexes; but the proportions, I am convinced, will be found to remain the same. As in the Razor-bill Auk, the excavation in the head of the *femur* for the round ligament is very small and shallow, and the neck of this part of the bone makes the same angle with the shaft as in that bird. This latter is but very slightly bent anteriorly, and has its muscular lines barely distinct. The outer condyle is the lower, and, owing to the superaddition of the usual fibular ledge, is the larger of the two. The shaft is for the most part nearly cylindrical on transverse section.

I find in *Uria* a well-developed *patella* in the ligament above the apex of the produced cnemial process, much as I have figured it for the Puffins, seen in figs. 52 and 53. In *Uria* it is not so large, however, and the groove for the ambiens muscle by no means so distinct as we find it in the Parrot Auks. Now, although it be missing in my specimen of *A. torda,* I think, from the similar construction of the bones of the leg, we can almost affirm with certainty that a patella such as we find in the Murres occurs also in the skeleton of the leg of the Razor-bill.

A *tibio-tarsus* has its cnemial process reared above the summit of the bone in the same way as I described and figured it for *A. torda;* upon its anterior aspect the pro- and ecto-cnemial ridges subside upon the shaft very soon after reaching it. This latter is smooth, straight, and sub-cylindrical on section. The fibular ridge is raised and roughened for that bone. Below we find the osseous bridge for the tendons going straight

across their groove, while in life an oblique ligamentous one is attached above this. The condyles are thin, far apart, and little produced upon the shaft posteriorly. Anteriorly they are thicker, more prominent, convex, and separated from each other by an intercondyloid fossa.

The tubercle on the *fibula* for the insertion of the tendon of the biceps is opposite the middle of the fibular ridge. Below, the extremity of this delicate bone anchyloses with the shaft of tibio-tarsus at about the junction of middle and lower thirds, at its external aspect.

Aside from its size, the *tarso-metatarsus* agrees in all innate characters with the same bone I figured for *A. torda*. If anything the hypotarsus is proportionately broader and not so prominent; additional material doubtless might modify this statement. It is simply grooved at its back for the passage of tendons. A like convex antero-median tubercle occurs at its summit, which in articulation passes between the condyles of the tibia.

The distal extremity bearing the trochleæ is essentially the same in all particulars as in the genus *Alca;* the same may be said of the phalanges of the toes.

I find, however, that in *Uria* the enlargement seen at the under side of each ungual phalanx exceeds in length half the joint, and these terminal osseous claws are but slightly curved evincing in their entire structure that feebleness in development which is so characteristic of them in pygopodine birds generally.

Brief Summary of the Osteological Differences between the Genus Alca and the Genus Uria.

In the analysis here presented I will simply submit such osteological characters as will probably prove to be constant ones, and from such only choose the differences that are found to exist between the skeletons of these two genera. From what has gone before, it will be easily surmised that the list will not be a long one.

Alca.—Superior mandible hooked at apex; laterally compressed; anterior half of culmen higher than posterior

and uniformly arched between tip of beak and its posterior commencement.

Uria.—Superior mandible not hooked; not compressed: culmen moderately arched and rounded, and entire mandible tapering uniformly to its apex.

Alca.—The hæmapophyses of the last pair of vertebral ribs but one articulate with the sternum; the last pair of vertebral ribs articulate with the sacrum; sternum has *eight* hæmapophysial facets on each costal border.

Uria.—The hæmapophyses of the last pair of vertebral ribs but one do not reach the sternum; the last pair of vertebral ribs fail to reach the sacrum; sternum has but *seven* hæmapophysial facets on each costal border.

Beyond these I know of no other characters, so far as the osteology of these two genera is concerned, that could with any propriety be entered in this synopsis. Suspicions of the commencement of deviation from which we may call, perhaps, the more standard type of either genus, I can see,—but these have no place in our analytical table; moreover, I have attempted, as we treated these skeletons in the foregoing paragraphs, to conveniently compare such minor specific differences and variations *en passant.*

So far as my material seems to indicate then, and from its consideration I am at present capable of judging, it would seem that this group of Auks, as they are arranged under the subfamily *Alcinæ* in the *A. O. U. Check-List*, is quite in keeping with our knowledge of their structure as it is now known to us. Their affinities as seen in their skeletons are quite clear, and I can only say that we would indeed be fortunate if we could find in other genera of birds in our fauna such evidences of kinship, accompanied by such excellent characters, to distinguish the genera.

I am of the opinion that *Alca* and *Plautus* are more nearly affined to each other than are *Alca* and *Uria*, but of the probable affinities of this last-mentioned genus of birds, we will have something to say in a later part of the present series of memoirs.

It is greatly to be regretted that all my efforts to secure a few skeletens of the *Alle alle* proved futile, and I consequently can say nothing in regard to the osteology of this sole representative of the subfamily *Allinæ*.

The only clue I have at hand to its structure is the superior view of its skull given by Garrod in his paper "On the Value in Classification of a Peculiarity in the Anterior Margin of the Nasal Bones in certain Birds" (*Proc. Zool. Soc.*, 1873, pp. 33-38, fig. 6). That figure I have compared with several skulls in my possession, and I find that although it has the supraorbital glandular depressions as in the *Alcinæ*, there is still much to remind us in its general form of the skull in such a type as *S. cristatellus*.

EXPLANATION OF PLATES VII.-XI.

[*Note.*—Although these Plates have a number of figures illustrating the osteology of the genus *Uria*, there are still others, as in the case of the shoulder girdle and some of the limb bones of *Alca torda*, that were described in Part I.; while, on the other hand, figures will be found here that will be fully described in future Parts of this work.]

Plate VII.

Fig. 1. Mandible of *Uria lomvia*, viewed from above; life size; by the author, from specimen 16,783 of the collection in the Smithsonian Institution.

Fig. 2. Skull of *Uria lomvia*, right lateral view; life size; by the author, from same specimen as in fig. 1.

Fig. 3. Skull of *Uria lomvia*, superior view with mandible removed; life size; by the author, same specimen as fig. 2.

Fig. 4. Skull of *Uria troile californica*, right lateral view; life size; by the author, from specimen 16,973 of the Smithsonian Collection.

Plate VIII.

Fig. 5. Left humerus of *Hæmatopus bachmani*, palmar aspect; life size; specimen 13,637, Smithsonian Collection; by the author.

Fig. 6. Left humerus of *Larus philadelphia*, palmar aspect; life size. Drawn by the author, from a specimen in his own collection.

Fig. 7. Sternum of *Urinator lumme*, pectoral view; life size; specimen 16,628, Smithsonian Collection. Drawn by the author.

Fig. 8. Left humerus of *Chionis minor*, palmar aspect; life size; specimen 16,950, Smithsonian Collection, Kidder's type specimen, and drawn by the author.

Fig. 9. Left humerus of *Charadrius dominicus*, palmar aspect; life size; by the author, from specimen 16,715 of the Smithsonian Collection (taken at Point Barrow, Alaska, Expedition of 1882).

Fig. 10. Left humerus of *Alca torda*, palmar aspect; life size; by the author, from the specimen presented him by Mr W. A. Forbes, F.Z.S.

Plate IX.

Fig. 11. Pectoral arch of *Alca torda*, inner aspect of the left lateral half; life size; by the author, from the Forbes specimen.

Fig. 12. Pectoral arch of *Larus delawarensis*; inner aspect of the left lateral half; life size; by the author, from a specimen in his own collection.

Fig. 13. Pectoral arch of *Chionis minor;* inner aspect of left lateral half; life size; by the author, from Dr Kidder's type specimen.

Fig. 14. Pectoral arch of *Hæmatopus bachmani*, inner aspect of left lateral half; life size; by the author, from specimen 13,637 of the Smithsonian Collection.

Fig. 15. Pectoral arch of *Urinator lumme*, inner aspect of left lateral half; life size; by the author, from specimen 16,628 of the collection in the Smithsonian Institution.

Plate X.

Fig. 16. Pelvis of *Alca torda* (the Forbes specimen alluded to in text).

Fig. 17. Pygostyle and the two ultimate caudal vertebræ; from same skeleton as fig. 16.

Fig. 18. Pelvis of *Larus delawarensis;* same specimen as used in former figures.

Fig. 19. Pygostyle and the three ultimate caudal vertebræ of *Larus delawarensis;* same skeleton as supplied the pelvis for fig. 18.

Fig. 20. Pelvis of *Chionis minor* (the type specimen of Dr Kidder's memoir, and alluded to throughout the text).

Fig. 21. Pelvis of *Hæmatopus bachmani;* from the same skeleton as elsewhere figured in these memoirs.

Fig. 22. Pygostyle and last caudal vertebra of the same skeleton of *Hæmatopus bachmani*, as alluded to in fig. 21.

All these figures are seen upon the right lateral aspect, and are drawn life size by the author from the specimens.

Plate XI.

Fig. 23. Pelvis of *Chionis minor.*

Fig. 24. Pelvis of *Alca torda.*

Fig. 25. Pelvis of *Hæmatopus bachmani.*

Fig. 26. Pelvis of *Larus delawarensis.*

These are all from the corresponding bones figured in Plate X. of this Part; all are by the author, and drawn life size from their dorsal aspects. Attention is invited to the greater similarity, so far as these parts are concerned, between *Chionis* and the Oyster-catcher and between the Auk and the Gull, rather than between *Chionis* and the Gull or Auk, or any other way we may choose to compare them.

ON THE ANATOMY OF *HYÆNA STRIATA*. By

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(*Continued from page 105.*)

PART II.

Myology.

IN Plates 129–142 of Cuvier and Laurillard's *Myology*, the muscular anatomy of *Hyæna striata* is fully illustrated, and descriptive accounts of individual muscles have been given by Meckel, Cuvier, and others. These accounts, however, are incomplete, and in not a few instances the muscles in our specimen were found to differ from the descriptions given. We have, therefore, thought it advisable to supplement the records of previous dissections of the muscular system of *H. striata* by that of our own, especially as, in so doing, we are able to avail ourselves for purposes of comparison of more complete descriptions of the muscles of the nearest allies of *H. striata* than was formerly possible.[1]

Muscles of the Head and Neck.—The *platysma myoides* and also the muscles of the face and of the auricles correspond in every respect with those of *H. crocuta.*

The muscles of mastication are also as described in the Spotted Hyæna with this exception, that the *masseter* is more easily separable into two layers. A well-defined tendinous lamina intervenes between the layers. Meckel states that this is less marked in Hyæna than in the Cat. Murie, however, found the muscle clearly divisible in *H. brunnea.*

The *sterno-cleido-mastoid* is arranged much as in other *Hyænidæ* and in *Proteles*, and differs from that of *Viverra Civetta*, in which the sterno-mastoid and cleido-mastoid are throughout distinct. As described in *H. crocuta* the fibres rise from the pro-sternum, and the muscle soon divides into two parts.

The fibres of the internal and larger portion arise in common

[1] See page 90, Part I.

with the corresponding fibres of the fellow-muscle of the opposite side, not only from the pro-sternum, but also from a tendinous raphe in the middle line of the neck, which extends from the pro-sternum to the larynx. In this way a muscular sling is formed for the soft tissues of the neck. The internal fibres converge to an insertion into the basi-occiput, whilst in *H. crocuta* they reach the base of the mastoid process.

The external and remaining portion of the muscle is inserted into the cervical fascia.

The *scaleni*, anterior *recti*, and *longus colli* muscles are exactly as in *H. crocuta*. The *splenius* of *H. striata* arises as in *H. crocuta*. The fibres from the spines of the first two dorsal vertebræ are, however, inserted into the third and fourth cervical transverse processes. In this respect *H. striata* agrees with *Viverra* and with the Dog, and differs from *H. crocuta* and *Proteles*, in which there is no splenius colli.

H. striata differs also from *H. crocuta* and *Proteles* in the possession of a *complexus*, divisible into complexus proper and digastric. There is, however, no complexus tertius as in *H. crocuta*, but there is a distinct trachelo-mastoid.

The *spinalis colli*, the posterior and lateral *recti*, and the *oblique* muscles are exactly similar to the same muscles in *H. crocuta*, as are also the strong, cervical, *intertransverse* muscle.

Muscles of Back, Thorax, and Abdomen.—The *panniculus carnosus* does not extend so far posteriorly or ventrally as in *H. crocuta*, but in other respects is similar.

The *trapezius* is small as in *H. crocuta* and *Proteles*, and is similarly limited in its origin to the ligamentum nuchæ and the anterior dorsal spines. In *H. striata*, however, the fibres are separated at their origin into two portions, a strong fibrous layer intervening; they are united at their insertion into the spine of the scapula. Meckel describes a trapezius in *H. striata*, consisting of two portions almost entirely separated, the posterior only of which corresponds to the trapezius of *H. crocuta*, and to that described by us, Meckel's anterior portion being regarded as the levator humeri.

The *latissimus dorsi* reaches back as far as the iliac crest, but in other respects is as in *H. crocuta*. It also gives off a dorso-epitrochlearis.

The *rhomboideus* is single. Meckel describes an occipital origin in *H. striata;* this does not exist in our specimen, which in this respect agrees with *H. crocuta*, *Proteles*, and *Viverra*.

The *serrati*, anterior and posterior, are quite distinct, as in *H. crocuta* and *Proteles*, whilst in *H. brunnea* and *Viverra* they are combined.

The *erector spinæ*, both as regards size and subdivision, resembles the same muscle in *H. crocuta* and *H. brunnea*. The outer column includes a *sacro-lumbalis* and a *musculus accessorius*. There is no *cervicalis ascendens*. In the Civet the latter muscle is feebly represented.

The *longissimus dorsi* is prolonged forwards by a strong *transversalis cervicis*, and there is a well-defined *trachelo-mastoid*. This latter muscle is not present in *H. crocuta*, but exists in *Viverra*. In *H. striata* it arises from the articular processes of the last five cervical and the first dorsal vertebræ, and is inserted into the mastoid process beneath the splenius capitis.

The *spinalis dorsi* is very large, and reaches the last two cervical spines.

The *multifidus spinæ*, *rotatores spinæ*, *interspinales*, and *levatores costarum* differ in no way from the account given in the description of *H. crocuta*.

The *serratus magnus*, the *intercostals*, the *triangularis sterni*, and the *diaphragm* are also as in *H. crocuta*.

The muscles of the abdominal wall are almost identical with those of *H. crocuta*. The *external oblique* has, however, only ten costal attachments. The *internal oblique* and *transversalis* are easily separable, and the latter muscle is limited to a zone skirting the posterior limit of the thoracic wall. There is no *pyramidalis*. The *rectus abdominis* is strong, and reaches from the pubes to the cartilages of the anterior seven ribs. The *supra costalis* is inserted anteriorly into the first rib, whilst in *H. crocuta* it is attached to the rib cartilage.

The *coccygeus*, *levator ani*, and tail muscles are as in the Spotted Hyæna.

Muscles of the Fore Limb.—The *pectoralis major* includes a superficial and a deep stratum of muscular fibres. It is much

as described by Meckel, and as in *H. crocuta*, but in our specimen the insertion of the superficial portion is even more extensive, and reaches from the great tuberosity down to the lower extremity of the humerus. The deep stratum is further divided into an anterior portion inserted into the tuberosity, and a posterior portion inserted into the shaft of the humerus.

There is no *pectoralis minor*.

Deltoid.—Meckel describes a deltoid in *H. striata*, consisting of two portions; one of these, however, forms part of the levator humeri. Including this element the deltoid in our specimen agrees with Meckel's description, and also with what obtains in *H. crocuta* and *Viverra*. Excluding this element the deltoid consists of fibres from the acromion, and of scapular fibres which arise from the fascia over the infraspinatus; these apparently constitute the clavicular portion of Meckel rather than those which form the levator humeri, as stated in the account of the deltoid in *H. crocuta*.

The *levator humeri proprius* arises as in *H. crocuta* by two heads, which unite in front of the shoulder-joint to form a strong fleshy mass. The insertion is into the ulna with the biceps; in this respect it apparently agrees with *H. brunnea*. In *Proteles* the insertion is into the radius and ulna, whilst in *H. crocuta* and in *Viverra* the insertion is into the lower end of the humerus.

The scapular muscles are arranged as in *H. crocuta*. The *teres minor* is small but distinct from the *infraspinatus*, so it is in *H. crocuta* and *Viverra*. In *Proteles*, on the contrary, these muscles are inseparable. A strong *teres major* is inserted, as in *H. crocuta*, *Proteles*, and *Viverra*, with the latissimus dorsi.

The *levator scapulæ* (trachelo-acromial) from the transverse process of the atlas is inserted into the acromion. In *Proteles* it is chiefly inserted into the fascia covering the infraspinatus. *H. crocuta* and *Viverra* agree with *H. striata*.

The *biceps*, though single headed as in *H. crocuta* and *Proteles*, arises from the margin of the glenoid cavity and from the rudimentary coracoid. It is inserted into both radius and ulna.

The *brachialis anticus* is inserted into the ulna alone, such

also is the case in *H. crocuta, Viverra,* and in the Dog. In *Proteles* the muscle is inserted into both radius and ulna.

The *coraco-brachialis* is a *C. brevis* (Wood) as in *H. crocuta, Proteles, Viverra,* and Cat.

The *triceps* is somewhat irregular in *Hyænidæ.* In *H. crocuta* four heads exist. So also in the Civet, whilst in *Proteles* a fifth head is described. In *H. striata* only three heads are distinguishable, a long scapular head, an outer head which corresponds to the second and third heads of *H. crocuta* conjoined, and an inner head, which is merely a small muscular slip from the inner border of the humerus near the insertion of the latissimus dorsi. The fourth head of this muscle in *H. crocuta* is in *H. striata* separate from the triceps, and combined with the *anconeus,* which extends from the posterior surface of the humerus for about an inch above the olecranon fossa, and from the back of the external condyle, to the outer side of the olecranon process.

There is no *supinator longus,* nor is there any tendinous vestige of this muscle such as is found in *H. crocuta. Proteles* resembles *H. striata* in this respect, but *Viverra* presents a small but well defined supinator longus.

Meckel rightly describes the *extensores carpi rad. longior and brevior* as separate and distinct throughout, the tendons of insertion being united by a transverse band.

The remaining extensor muscles of the wrist and digits, and also the *supinator brevis,* are arranged exactly as in the Spotted Hyæna, with this exception, that the *extensor indicis* in *H. striata* is distributed to the index, middle, and ring digits, whereas in *H. crocuta* it is limited to the first of these.

The two *pronator* muscles of the fore-arm are also precisely as in *H. crocuta* and *Proteles.* In the Civet the pronator quadratus is much more limited, whilst the pronator teres is relatively larger and stronger.

Of the radial and ulnar flexors of the wrist the former is as described in *H. crocuta,* the latter (*flex. carp. ulnaris*) has, however, both humeral and olecranoid heads, and beyond its connection with the pisiform bone is prolonged to the outer metacarpal bone. Meckel found the prolongation more extensive, and noted its ligamentous connection with the four outer

metacarpal bones. Meckel states that the palmaris longus in Hyæna and the Bear is intimately united with the superficial flexor of the digits. In our specimen it is quite separate as in *H. crocuta* and *Proteles*. In *Viverra* it is double, and forms two slender muscles.

Flexores digitorum.—The superficial and the deep flexors form a large muscular mass closely resembling the corresponding structure in *H. crocuta, Proteles*, and *Viverra*. The muscular fibres, however, arise exclusively from the humerus and ulna, and there is no radial attachment. One group of fibres from the humeral condyle is prolonged as the superficial flexor, its deeper fibres join the deep flexor, which obtains additional fibres from the humerus, from the coronoid process and from the whole length of the posterior border of the ulna; the last named fibres are supplied by the ulnar nerve, whilst the nerve supply of the rest of the mass is derived from the median. The flexor perforatus or superficial part of the muscle ends in four tendons, which are distributed to the four outer digits; before their insertion into the second phalanges they form tubular sheaths for the deep flexor tendons which pass to the terminal phalanges of the same toes. Meckel found the superficial flexor of the outermost digit springing from the palmar fascia, and he describes from an expansion of this head accessory slips distributed to the superficial tendons which aid in the formation of the sheaths for the deep tendons. In our specimen, however, there is no such arrangement, but slender accessory slips pass directly from the palmar fascia to the superficial flexor tendons.

Meckel affirms the existence in Hyæna of a very small and thin *flexor longus pollicis*. We were unable to verify this statement. The muscle is also absent in *H. crocuta*, and in *Proteles* it is not separable from the deep flexor.

Lumbricales.—There are only two lumbricales. They are connected with the deep flexor tendon before its division, and with the superficial flexor tendons of the middle and ring digits. This arrangement is precisely the same as in *H. crocuta*, in which, however, there are four lumbrical muscles. In *Proteles* there are only three. In the Civet four lumbrical muscles exist, but they have no connection with the superficial flexors.

The intrinsic muscles of the hand include—

1. A palmar group of adductors.
2. An intermediate group of flexors.
3. A dorsal group of abductors.

The palmar group consists of an *adductor minimi digiti* and an *adductor indicis*. The first named is thin and flat; it rises, superficial to the adductor indicis, from the palmar surface of the carpus about the middle line, and passes to the radial side of the proximal phalanx of the outermost digit. The adductor indicis arises beneath the adductor minimi digiti by two heads, one from the middle of the carpal ligaments, the second from the radial side of the origin of the flexor brevis of the ring digit. The two heads are separated by the deep division of the ulnar nerve.

The intermediate layer of *flexores breves* is made up of four strong double bellied muscles; the muscular bellies are arranged in pairs along each metacarpal bone. Arising from their proximal ends by single pointed tendinous origins, they pass to the bases of the first phalanges, reaching as far as the extensor tendons.

The dorsal layer is represented by a single muscle, the *abductor minimi digiti*, which passes from the pisiform bone to join the extensor expansion on the first phalanx of the fifth digit. In *H. crocuta* there is no adductor indicis, but there is an adductor of the middle digit; in other respects it resembles *H. striata*. *Proteles* also agrees with the latter.

Nerve Supply of the Muscles of the Anterior Extremity.—Of special interest in the nerve supply of the muscles of the upper extremity is the fact that the musculo-cutaneous nerve, besides supplying the biceps, coraco-brachialis, and brachialis anticus, also gives branches of supply to the flexor carpi radialis and the pronator teres. The flexor carpi ulnaris and the ulnar origin of the deep flexor are supplied by the ulnar nerve; with these exceptions all the muscles on the front of the fore-arm are supplied by the median.

The lumbrical muscles, which correspond to the second and third of the human hand, are both supplied by the median nerve.

The ulnar nerve supplies all the intrinsic muscles of the hand.

In a recent paper on the "Nerve Supply of the Lumbrical Muscles of the Hand and Foot,"[1] Dr H. St John Brooks suggests that a struggle is going on between the median and ulnar nerves for the possession of the intrinsic muscles of the hand, including the lumbricals, and he advances the hypothesis that the pressure to which the superficial nerve (the median) is exposed places it at a disadvantage, and that as a consequence it is losing its grasp over some of the muscles, which are gradually passing into the domain of the deep nerve (the ulnar). It is perhaps not very important which nerve supplies these muscles, as it is clear from the researches of Ferrier and Yeo,[2] and Herringham,[3] that they are supplied by the eighth cervical, and perhaps the first dorsal nerve, fibres of which are found both in the median and ulnar nerves,[4] but it is certain that pressure can have nothing to do primarily with the change of supply; for the nerves are in position before the muscles are differentiated from the mesoblastic matrix of the limb, and the branches of the nerves become connected with the muscles long before any pressure is brought to bear on the extremities. Further, as the nerves are in position before the muscles are developed, any change in the supply of a muscle must be due to an alteration in the number of fibres which pass to form the trunks of the respective nerves at the time when, as Paterson[5] has shown, the ventral branches of the spinal nerves in the region of the upper extremity have formed a plexus from which fibres proceed for the formation of the various peripheral nerves. Thus the contest resolves itself into a struggle between two nerves, as yet non-existent, for the possession of the fibres which are eventually to form them.

Accepting as correct the statement that the domain of the ulnar nerve is gradually increasing at the expense of that originally belonging to the median, the occurrence is probably due to the perpetuation of an accidental variation which has proved serviceable to the possessor. Such a variation may have

[1] *Jour. of Anat. and Phys.*, vol. xxi.

[2] *Proceedings of the Royal Society*, Mar. 1881.

[3] *Proc. Roy. Soc.*, vol. xli. 1886.

[4] Quain, vol. i. 1882, p. 606.

[5] "On the Fate of the Muscle Plate," *Quart. Jour. Mic. Sci.*, vol. xxviii.

occurred in one of two ways. Either the myotomes involved in the constitution of the muscles may have varied, and as each myotome is supplied by its own nerve this would necessarily be associated with a change of nerve supply; or, as is more probable, the variation is due to a change in the course of some of the fibres passing from the brachial plexus to the median and ulnar nerves. Thus, after the eighth cervical nerve unites in a plexus with the other nerve going to the fore limb, its fibres may pass into any of the peripheral trunks, and if fibres which at one time passed into the median nerve, are at another directed into the ulnar, the domain of the latter will be increased at the expense of that of the former.

Muscles of the Hind Limb.—Except that in *H. striata* the posterior portion of the *gluteus maximus* joins the biceps flexor cruris much sooner than in *H. crocuta*, the gluteal group of muscles and the tensor fasciæ femoris are alike in the two species. Meckel noted the existence of a gluteus quartus in *H. striata.*

The deeper placed external rotator muscles, *e.g.*, pyriformis, obturator internus and gemelli, obturator externus and quadratus femoris, are arranged as in *H. crocuta* and *Viverra*, but in *Proteles* there is only a single gemellus.

The *semimembranosus*, not unfrequently united, in Carnivores, more or less closely with the adductor mass, is, as Meckel describes, separate and distinct. It is also separate in the Civet, whilst in *H. crocuta* and *Proteles* it is inseparable from the adductor magnus.

The *semitendinosus* is inserted into the anterior border of the tibia immediately below the tubercle; apparently this insertion is higher and more anterior than was found by Meckel.

The *biceps* arises from the ischial tuberosity, and is joined by fleshy fibres from the anterior three caudal vertebræ, which constitute the posterior part of the double gluteus maximus of *H. crocuta.*

The *sartorius* is double, as in *H. crocuta;* the outer portion joins the rectus, and constitutes an additional element in the common extensor of the knee. In *Proteles* and *Viverra* the sartorius is single.

The *adductor magnus* is not united with the semimem-

branosus as in *H. crocuta*, and, consequently, its insertion is solely femoral. The *adductor brevis*, the *gracilis*, and *pectineus* are exactly as described in the Spotted Hyæna.

The *rectus femoris* in *H. crocuta* and *Viverra* arises by two heads. In *H. striata* and in *Proteles* the two heads are not distinct. There is no differentiated crureus, but the *vasti* muscles are easily separable.

The *gastrocnemius* is well developed, but the soleus is wanting; so also in *H. crocuta* and *Proteles*. In *Viverra* a separate and distinct soleus exists.

The *plantaris* has no attachment to the os calcis but is prolonged into the sole, where it divides into four slips, one for each toe. Each slip is strengthened by processes from the plantar fascia, is subsequently perforated by a corresponding tendon of the flexor perforans, and is ultimately inserted into the second phalanx of the toe. This represents the *flexor brevis digitorum* (perforatus). The accessory muscular fibres from the fourth metatarsal bone, noted by Meckel, are not present in our specimen. In *H. crocuta* and *Proteles* the plantaris ends at the os calcis; in the former of these there is a separate tendinous flexor brevis digitorum, which is confined to the sole of the foot. In *Proteles* the flexor brevis is also tendinous, but is continuous at its origin with the plantaris tendon. The Civet corresponds more closely to *H. striata*, but receives accessory muscular fibres from the os calcis.

The *flexor longus digitorum* (perforans), together with the flexor longus hallucis, is arranged and attached as in the Spotted Hyæna. The *popliteus* and *tibialis posticus* are also similar.

A musculus accessorius is not present in *H. striata*. It exists in *H. crocuta*, also in *Viverra*, but is absent in *Proteles*.

The *lumbricales* are three in number, but two pass to the superficial flexor tendon of the middle toe; and of these one—the second—is tendinous. The third lumbrical goes to the superficial flexor of the ring digit. The arrangement is very similar in *H. crocuta*. In *Proteles* there are three lumbricals which pass to separate toes, while in *Viverra* four lumbricals are distributed in the usual manner.

The intrinsic muscles of the foot are represented by two layers, the palmar layer of adductors and the intermediate layer

of flexors. There is no dorsal layer of abductors, and no trace of fusion of the abductor minimi digiti with the short flexor of the little toe, similar to that described by Cunningham in the Dog,[1] could be found.

As in the hand, the palmar group of adductors is represented by two small muscular bundles, one an adductor of the little toe, the other of the index digit. These two muscles bear the same relative positions to each other as in the hand, and similarly the adductor of the index digit has a double origin, the two heads are separated by the continuation of the external plantar nerve to the flexor brevis indicis.

The intermediate layer of short flexors is constituted by four bicipital muscles, each single at its origin from the base of the metatarsal bone on which it lies; the separation of the two bellies is low down, and each of these is inserted into the sides of the first phalanx of the same toe and into the extensor expansion. Cunningham ascribes the absence, in some animals, of the dorsal layer to its fusion with a primitively separate intermediate layer. In *H. striata* there is no trace of this fusion.

The *extensor longus digitorum* does not divide into two distinct bellies, as Meckel found in his specimen, but is single, as in *H. crocuta*, *Proteles*, and *Viverra*.

The *tibialis anticus* is a single muscle inserted into the metatarsal bone of the second toe. There is no extensor hallucis; in *Proteles* and in *H. crocuta* a slip from the tibialis anticus represents this muscle, whilst in *Viverra* a separate extensor hallucis proprius exists.

The *extensor brevis digitorum* terminates in four tendons. Of these, the first is to the second toe, the second and third to the third toe, and the fourth tendon goes to the fourth toe, but gives also a slender slip to the fifth toe. Meckel found three tendons only, distributed as in *H. crocuta*. In *Proteles* two tendons pass to the second and third toes respectively. In the Civet four tendons are distributed to the four inner toes, whilst in the Dog they pass to the four outer toes.

The *peroneal* group of muscles usually includes, in Carnivora,

[1] "Intrinsic Muscles of the Mammalian Foot," *Jour. of Anat. and Phys.*, vol. xiii. p. 9.

a peroneus longus, peroneus brevis, and extensor quinti digiti. It is not uncommon, however, for the last two muscles to be more or less united, as, *e.g.*, in *H. crocuta* and the Dog. In *H. striata* these muscles are separate.

The *peroneus longus* arises from the upper extremity of the tibia and the external lateral ligament of the knee-joint, in this respect intervening between *H. crocuta*, Nasua, and the Badger on the one hand, in which the peroneus longus rises from the external condyle of the femur, and *Proteles*, the Civet, the Lion, and the Wolf on the other, the muscle in the latter group of animals gaining origin from the head of the fibula and the fascia of the leg. The second head of origin, which, as found by Ruge [1] in *Mustela* and *Leo*, is separated from the first by the peroneal nerve, is not present in *H. striata*. The tendon of insertion passes over the front of the external malleolus, a position generally found in Carnivora; it then crosses the peroneus brevis, giving a strong slip to the base of the fifth metatarsal bone, and passes across the sole to reach the second metatarsal.

The insertion of the muscle appears to vary greatly in Carnivores. In *H. crocuta* and *Proteles* it is attached to the fifth metatarsal only, in the Civet to the first and fifth, in the Fox and Dog to the cuboid and fourth and fifth metatarsals.

Ruge states that in Carnivora the *peroneus brevis* usually rises from the lower portion of the fibula, and this is certainly true of *H. striata*. In *Viverra*, however, it rises from the upper two-thirds of the shaft, and in *H. crocuta* from the middle portion. Its tendon passes behind the external malleolus, and is inserted into the base of the fifth metatarsal bone. This insertion seems to be universal in Carnivora.

The *extensor quinti digiti* takes origin from the head of the fibula, and from the shaft of the bone above and behind the peroneus brevis. Its tendon of insertion passes behind the external malleolus, and then divides into two parts, one of which is inserted into the base of the fifth metatarsal bone, whilst the other joins the extensor expansion on the fifth toe. The muscle is absent in *H. crocuta*, but is very generally present in Carnivores.

[1] *Morph. Jahrbuch*, 1878, Bd. iv. p. 617.

Nerve Supply of the Muscles of the Lower Extremity.

The muscles of the buttock and the front and back of the thigh are supplied in the usual manner.

We are able to confirm Ruge's[1] description of the peroneal nerve in Carnivora, and to distinguish the branches which he has named deep, superficial, and accessory. The latter, in *H. striata* as in *Mustela*, ends in the peroneus brevis, after supplying the extensor of the fifth digit. The deep peroneal branch supplies the short extensors of the toes. The muscles of the back of the leg are supplied by the posterior tibial nerve. The deep branch of the external plantar supplies the intrinsic muscles of the foot. The lumbricales are supplied by the internal plantar.

The intrinsic muscles of the hand and foot have been described as forming palmar, dorsal, and intermediate groups—a method of classification which has been most ably advocated by Professor Cunningham,[2] to whom it is mainly due. Cunningham looks upon the tri-laminar arrangement as "typical," and considers that each digit should be furnished with three independent muscles, one from each layer, the medius being an exception, since it obtains two muscles from the dorsal layer; and he considers that "deviations from the typical arrangement of these muscles take place, in the majority of cases, either by suppression or fusion of certain elements of the different layers."

It has been already pointed out[3] by one of us that the typical arrangement is met with in its most complete form in animals whose extremities are highly specialised for grasping, holding, and manipulating; and, more particularly, that individual elements of the groups are always best developed in connection with the digits which have become most individualised.

Want of knowledge of the steps by which these muscles are developmentally produced, and the insufficiency of observations on their adult condition, render it impossible at present to arrive at definite conclusions concerning them; but the facts so far obtained seem to show that the type arrangement described by Cunningham is typical of the highest form of muscular

[1] *Morph. Jahrbuch*, Bd. iv.

[2] *Loc. cit.*, p. 2.

[3] Young, "Intrinsic Muscles of the Marsupial Hand," *Jour. Anat. and Phys.*, vol. xiv. p. 160.

differentiation yet arrived at, and that, although there is no doubt that in some cases, due to change of circumstances in the life-history of groups of animals, variations from the typical or tri-laminar arrangement of the muscles will be found that are due to suppression or fusion; still, as a general rule, when any of the various groups are wanting, their absence must be imputed to non-differentiation rather than to suppression or fusion. For, as it is certain that the intrinsic muscles of the hand and foot—we speak from careful examination of the hands and feet of human embryos and the embryos of rats and mice—are differentiated from an uniform mass of mesoblastic cells, and as the ontogenesis of the individual represents to a great extent the phylogenesis of its class, we cannot but deem it improbable that Nature would depart so far from her ordinary course of evolving the more perfect from the less perfect as to produce suddenly, a highly differentiated typical series of muscles from which most of her future elaborations should deviate by degeneration.

Again, it is at times difficult, when the various muscles have wandered from their origin, or are more or less inseparable from their neighbours, to say to which group they belong. Ruge,[1] in his paper "On the Intrinsic Muscles of the Foot," states that all the muscles lying superficial to the deep branch of the external plantar nerve belong to the palmar or adductor group; Brooks[2] supports this statement, and applies a similar law to the muscles of the hand, the deep branch of the ulnar nerve being taken as the separating structure. If this be the case, then the adductor of the index digit in the hand of *H. striata*, and the adductor of the corresponding digit in the foot, must be looked upon as being derived partly from the adductor and partly from the flexor layers, for, as we have shown, it takes origin by two heads, one of which is superficial to the deep nerve, whilst the other, which rises from the fascia on the radial side of the flexor of the ring digit, is deeper than the nerve; as, however, the muscle is single at its insertion, and as from the direction of its fibres it is an adductor muscle, we have placed it in the palmar group.

[1] *Morph. Jahrbuch*, Bd. iv. p. 645.

[2] "Morphology of the Intrinsic Muscles," *Jour. Anat. and Phys.*, vol. xx.

THE GUSTATORY ORGANS OF *VULPES VULGARIS*.

By Frederick Tuckerman, M.D., *Amherst, Massachusetts.*

Before passing to the consideration of the taste-organs of *Vulpes*, I will describe briefly the form and external appearance of the tongue of this mammal.

The tongue is long, comparatively narrow, flat, and a little expanded anteriorly, and terminates in an obtuse apex. It measures 120 mm. in length, 20 mm. in breadth, and 15 mm. at its thickest part. It is free from the floor of the mouth for 45 mm.

The upper surface resembles fine shagreen, and the small fungiform papillæ which are scattered over the greater part of the dorsum give it the appearance of being studded with minute white beads. It is impressed for nearly its entire length by a very shallow longitudinal median groove, which disappears near the base and tip. About the root and extreme posterior borders are thick, coarse, fleshy, recurved, cone-shaped papillæ. The rest of the dorsal surface is covered with small, closely-set, cone- or club-shaped mechanical papillæ, having their apices directed backwards. When stroked in the opposite direction, these papillæ convey the feeling of a fine-toothed rasp. Each papilla is seated upon one or two papillary upgrowths of the mucosa, and has from one to three minute spines projecting from its upper surface. The papillæ are largest and most thickly placed at the posterior part of the dorsum, and decrease in size towards the tip, where they also lose their spinules to a great extent. At the back of the tongue they measure about 0·80 mm. in height and 0·40 mm. in breadth. The epithelium sheathing the papillæ is partially, and that composing the spinules entirely, cornified.

The fungiform papillæ are abundant, and are distributed quite uniformly over the upper surface and sides from the tip to the gustatory area. They are smallest and closest set at the fore part of the dorsum, the anterior edge being thickly beset

with them, and they gradually increase in size as they recede from the tip and approach the base of the organ.

The circumvallate papillæ, of which there are two pairs,—an anterior and a posterior,—are situate well back on the dorsum, a few millimetres from the median line. They are small, somewhat concealed, and lie slightly below the level of the adjacent surface. The posterior pair, the larger of the two, are 21 mm. from the base of the tongue, and 7 mm. from each other. The anterior pair are 1 mm. distant from the posterior, and are 9 mm. apart. At each side of the base of the tongue, immediately in front of the glosso-palatine arch, is a papilla foliata.

The mucous membrane of the under surface of the tongue is here and there thrown into small transverse folds, having a subparallel arrangement, and which are more noticeable near the lateral margins.

Gustatory Areas.

The Circumvallate Papillæ.—The adjoining surface surrounding this taste-area is covered with papillæ of both tactile and mechanical function. The latter are mainly cone-shaped, and terminate in a recurved pointed extremity.

A noteworthy and interesting feature of these papillæ is presented in the appearance of their upper part. In vertical sections this is seen to be cleft. The depth of the fissure varies greatly in different parts of the same papilla, and sometimes extends from the summit half-way to the base, leaving a wedge-shaped space partially filled with epithelium. Comparison of vertical and horizontal sections of the circumvallate papillæ show them to be distinctly lobate in their upper portion, there usually being one large lobe and one or two smaller ones to a single papilla. The posterior pair are more distinctly cleft, and more inclined to lobation than the anterior. They measure 1·5 mm. in their transverse diameter, and are about 0·80 mm. in height. Each papilla is encircled by a deep and narrow trench of uniform width. Serous glands are not abundant, and are only very sparingly present within the papillary body itself. Their ducts open into the trench at its base and sides. At the base of the papilla, the nerves, which at first are chiefly medulated, but finally lose their medullary sheath, form a plexus.

From this plexus fibres enter the papilla and ramify throughout it. In the submucosa underlying the gustatory region fat is very abundant, either massed in smaller or larger groups of fat cells, or in the form of lobules between the bundles of muscular fibres, or, in some instances, separating the individual fibres themselves.

The taste-bulbs of this area are quite plentiful. They are disposed at the sides in a zone of sixteen tiers, the uppermost tier occasionally being well up towards the top of the papilla. Rarely, isolated bulbs are present in the epithelium of the free upper surface. Taste-bulbs are also present in the lower part of the outer wall of the trench. Here they are arranged in a girdle of ten tiers. When viewed in horizontal section the bulbs of this area are very beautiful. They are generally in contact by their edges, and thus form a nearly unbroken belt around the free border of the papilla. From horizontal sections, made at different levels, I estimated the number of bulbs in a tier at 120. Those of the outer wall, though normally present, are more irregular in their distribution and arrangement, and the number visible in a horizontal section is much less than in the papilla proper. The total number of bulbs divided between the four papillæ comprising this gustatory area cannot, I think, be less than 9500.

The bulbs, like the papillæ which lodge them, are smaller than would be expected in an animal of this size.[1] They measure 0·042 mm. in length and 0·020 mm. in breadth. The gustatory pores vary in shape as well as in size. One that I measured was 0·0025 mm. in diameter.

The Foliate Papillæ.—The papillæ foliatæ of *V. vulgaris* are so inconspicuous that they might easily be overlooked. They lie deeply embedded in the tongue, their ridges scarcely reaching the surface, while externally a fringe of papillæ serves quite effectually to conceal their presence.

Each papilla consists of eight to fourteen quite regular folds, having the same general appearance but varying somewhat in size. The furrows separating the folds are narrow, with a nearly

[1] The Table on p. 205, appended to this paper, contains some comparative data respecting the taste-organs of a number of mammals, several of which are widely separated generically.

uniform breadth throughout, and have an average depth of about 1 mm. The folds do not culminate in a rounded or flattened crest, as is usual, but are prolonged into, or surmounted by, rather coarse, sharp, retroverted spines. These spines are from 0·25 to 0·50 mm. in height, their basal diameter being generally a little less than their height. The epithelium covering them is imbricated in arrangement, and in the superior part of the spine is either partly or wholly cornified.

From their structure it is evident, I think, that the function of these spines is a purely mechanical one; and it is probable that they serve to arrest particles of gustable matter that come in their way long enough for them to fall into the furrows, where they are bathed in the secretion of the serous glands, and come in direct contact with the free ends of the taste-cells.

The folds are, for the most part, simple in construction. Serous glands and ducts are fairly abundant about their base, and the latter usually open at the bottom of a furrow. Sections through some regions of these papillæ reveal now and then a furrow which is completely closed at its upper part by stratified pavement epithelium. In the crypt-like space thus formed bulbs are numerous lining the sides, and serous ducts discharge at the bottom of the crypt. The inferior part of the foliate papilla, or that portion nearest the under lingual surface, is the most irregular in its development. The folds lack symmetry of form, the spines are wanting, and the furrows are of varying width and shallow.

The taste-bulbs of this area are in general confined to the lower half of the folds, although detached bulbs not infrequently occur on the free upper surface. They are very numerous, there being sometimes twenty or more tiers of them. I was unable to obtain good horizontal sections of this papilla, and am thus unable to state the approximate number of bulbs distributed to this area. The bulbs do not differ save in size (being a trifle smaller) from those of the circumvallate papilla.

The Fungiform Papillæ.—These papillæ are numerous, and are distributed quite regularly over the dorsum and sides of the tongue. Some of them rest in a shallow depression of the mucous membrane, and resemble, in some degree, papillæ of the circumvallate type. Taste-bulbs are present in the epithelium of the

upper part of these papillæ. In a horizontal section I counted nine bulbs which had been divided transversely to their long axis. They measure 0·038 to 0·045 mm. in length and 0·021 to 0·024 in breadth. Most of the bulbs examined communicate freely with the surface either directly or by means of a tube or neck leading to an opening in the outer layer of epithelium. Many of the bulbs appear not to touch the mucosa at any point, but to be entirely epithelial in position.

TABLE.[1]

	Number of Circumvallate Papillæ.	Number of Bulbs in Circumvallate Papillæ.	Mean Dimensions of Bulbs.		Papilla Foliata.	Number of Bulbs in Papilla Foliata.	Mean Dimensions of Bulbs.	
			Length.	Greatest Transverse Diameter.			Length.	Greatest Transverse Diameter.
			mm.	mm.			mm.	mm.
Bandicoot (*P. nasuta*).	3	2,160	0·070	0·043	Wanting	...	...	...
Bat (*V. subulatus*).	2	800	0·026	0·014	Do.	...	...	...
Musk-Rat (*F. zibethicus*).	1	520	0·050	0·027	Present	800	0·046	0·027
Rabbit, . .	2	2,400	0·050	0·033	Do.	14,500	0·055	0·036
Horse, . .	2	...	0·080	0·070	Do.	...	...	...
Pig, . . .	2	10,760	0·092	0·036	Do.	4,800	0·066	0·033
Sheep, . .	24	9,600	0·085	0·045	Wanting	...	...	...
Calf, . .	24	35,200	0·100	0·040	Do.	...	...	...
Goat, . .	12	15,400	0·062	0·030	Do.	...	...	...
Cat, . .	6	600	0·070	0·032	Do.	...	...	...
Dog, . .	4–6	...	0·071	0·040	Present	...	...	...
Fox (*V. vulgaris*).	4	9,500	0·042	0·020	Do.	...	0·045	0·021
Skunk (*M. mephitica*).	2	4,000	0·045	0·028	Wanting	...	...	...
Mink (*P. vison*).	4-5	2,000	0·039	0·024	Rudimentary	...	...	...
Man, . . .	9	6,000	0·079	0·040	Present	3,000	0·070	0·038

[1] The Ornithorhynchus, although omitted from the Table for want of sufficient data, should be mentioned on account of its highly ancestral character. At the posterior region of the tongue of this mammal are two pairs of taste-areas. The anterior pair lie below the surface in a furrow, the floor of which is invaginated upwards into a ridge, which bears the taste-bulbs. The ridges of the posterior pair reach the surface. On one of the ridges Poulton estimated the number of bulbs, to the square millimetre of surface, at about 500.

THE HOMOLOGY AND INNERVATION OF THE ACHSELBOGEN AND PECTORALIS QUARTUS, AND THE NATURE OF THE LATERAL CUTANEOUS NERVE OF THE THORAX. By AMBROSE BIRMINGHAM, M.B., *Professor of Anatomy, Catholic University, Ireland.*[1]

THERE are occasionally found in the region of the shoulder in man two inconstant muscles, the true nature of which, judging by the views of different anatomists on the subject, is not quite settled. The muscles I refer to are the achselbogen of Langer, more commonly known as a muscular axillary arch, and the pectoralis quartus. The first (found once in every sixteen subjects, according to Professor Macalister,[2] or in 7 per cent. of the bodies examined, according to Krause[3]) is a narrow band, generally muscular, passing from the posterior to the anterior fold of the axilla. The second is a rare muscle in the human subject, but is commonly found in animals; it runs along, or under cover of the lower margin of the pectoralis major, from the thorax to the upper part of the arm.

With regard to the achselbogen, the following views have been put forward:—(1) Mr Galton[4] considered it the representative in the human subject of the pectoralis quartus in animals, a view supported by Professor Macalister.[5] (2) Mr J. B. Perrin[6] is of opinion that the achselbogen is an "aborted variety of the dorso-epitrochlearis," which latter he regards as an "aborted specimen of the panniculus," or a "representative of the dorso-humeral portion of the panniculus." (3) According to Professor Humphry,[7] the achsel-bogen is due to the imperfect segmentation of the pectoralis major from the latissimus dorsi, or of the ventral from the dorsal portion of the superficial brachio-cephalic muscular sheet, being as it were a partial reversion to the condition in Lepidosiren, where the two muscles are continuous with each other. And, lastly, there is the

[1] This paper was read before the Anatomical Section of the Royal Academy of Medicine, Ireland, in March 1888.

[2] *Trans. Roy. Irish Acad.*, 1872.

[3] Quoted by Mr J. T. Wilson, *Jour. Anat.*, vol. xxii.

[4] *Linn. Trans.*, vol. xxi.

[5] *Ann. and Mag. Nat. Hist.*, July 1869.

[6] Mr Wilson, *Jour. Anat.*, vol. xxii.

[7] *Observations in Myology*, p. 131.

view suggested by Sir William Turner,[1] and supported by Mr J. T. Wilson,[2] that the achselbogen is a representative of the panniculus. As to the pectoralis quartus, it was considered by Mr Galton, as mentioned above, to correspond to the achselbogen. Mr Wood[3] suggested that it was an imperfectly developed slip of the dorso-epitrochlearis. Professor Owen[4] regarded it as a differentiated portion of the great pectoral, and Professor Macalister,[5] in confirmation of this view, says,—"This muscle I consider to be a fourth pectoral, and its insertion is, I think, sufficient to determine this relation." Lastly, Professor Humphry[6] describes a muscle, which he calls the brachio-lateralis, as a portion of the panniculus, but the brachio-lateralis of Professor Humphry is the pectoralis quartus of other authors (according to Professor Macalister),[7] therefore we may infer that Professor Humphry considers the pectoralis quartus a derivative of the panniculus. In the "Challenger Reports"[8] Professor Cunningham expresses a similar passing opinion.

Thus we see there are four different views held by anatomists regarding each of the muscles under consideration: to solve the question, which are we to adopt? I propose to examine the different theories *seriatim*, testing each, when necessary, by the following criteria of homology, position, origin, insertion, and, most important, nerve-supply.

First, I shall take up the pectoralis quartus. Professor Macalister, in his "Muscular Anomalies,"[9] describes the pectoralis quartus as a muscle rarely present in man, which, arising from the lower ribs and lateral thoracic fascia, runs along the lower margin of the great pectoral, and is inserted into the humerus with or below the pectoralis major, or into the fascia of the upper part of the arm alone. Its nerve in man comes from the internal anterior thoracic (Dr Brooks kindly supplied me with notes of some dissections, in which he found the nerve thus derived). Dr W. H. Thompson has found in the Sloth Bear, and I in the Dog, Cat, Macaque Monkey, and Man, the muscle supplied by the same nerve. The first theory I have mentioned with regard to the homology of this muscle is Mr Galton's, namely,

[1] *Jour. Anat.*, vol. i., *footnote* p. 252, 1867.
[2] Mr Wilson, *Jour. Anat.*, vol. xxii., 1888.
[3] Macalister, *Ann. Nat. Hist.*, July 1869.
[4] *Ibid.* [5] *Ibid.*
[6] *Observations in Myology*, p. 132.
[7] *Ann. Nat. Hist.*, March 1870.
[8] Vol. v. part xvi., 1882.
[9] *Trans. Roy. Irish Acad.*, 1872.

that the pectoralis quartus corresponds to the achselbogen. That this is not so is proven at once, I think, by the fact that in two cases—the notes of which Dr Brooks has kindly sent and me—the pectoralis quartus and achselbogen were both present, and each occupied its usual position; further, at its pectoral end the achselbogen was connected with the pectoralis quartus instead of with the great pectoral as usual. Later on, when we find the true nature of the achselbogen, other reasons for opposing Mr Galton's view will become apparent.

Next comes Mr Wood's idea that the pectoralis quartus is an imperfectly-developed slip of the dorso-epitrochlearis. That this is not correct, Mr Galton argues, from the fact that the dorso-epitrochlearis and pectoralis quartus are both present, and distinct in many animals, and his argument is supported by Professor Macalister.[1] The dorso-epitrochlearis usually springs from the latissimus dorsi at the junction of tendon and muscle, passes down the inner side of the arm, and is inserted in the region of the inner condyle or olecranon. At once we see it does not correspond with the pectoralis quartus in origin, insertion, or position. The same may be said with regard to nerve-supply. In the Chimpanzee the dorso-epitrochlearis is supplied by the musculo-spinal nerve, according to Mr Champneys,[2] and I have found it supplied virtually by the same nerve in the Macaque, Dog, and Cat. Hence we see that in nerve-supply, as well as in the other criteria proposed, the dorso-epitrochlearis and pectoralis quartus disagree, and they evidently are not homologues.

Lastly, we have the views of Professor Owen and Professor Humphry; the former considers the muscle a differentiated portion of the lower border of the great pectoral, and, with such a segmented slip, it agrees in origin, position, insertion, and nerve-supply; it corresponds in every detail with the lower border of the pectoral. On the other hand, testing Professor Humphry's view,—that the quartus is derived from the ventral part of the humeral panniculus,—we find that the pectoralis quartus agrees with this portion of the panniculus in position, insertion, and indeed, we might add, in origin, for a thickened band of the panniculus is found in many animals—for instance

[1] *Ann. Nat. Hist.*, 1869. [2] *Jour. Anat.*, vol. vi. p. 180, *footnote*.

the Rabbit—running along the axillary margin of the pectoralis major from the ventral aspect of the thorax and abdomen to the arm, and this band looks remarkably like a pectoralis quartus. But in nerve-supply there is an apparent difference: the panniculus is supplied by the "lateral cutaneous nerve of the thorax,"[1] which is said by Dr A. M. Paterson[2] to be the homologue of the nerve of Wrisberg, the quartus by the internal anterior thoracic; these statements weigh heavily against Professor Humphry's theory if they be accurate, but I hope to be able to show later on, in connection with the achselbogen and its nerve-supply, that this difference in innervation is little more than apparent. For the present, then, we may consider that both views present nearly equal claims for adoption on the grounds of position, origin, insertion, and nerve-supply. The following considerations may help us to decide which is the correct view to be taken:—(1) In the Kangaroo and Wallaby the pectoralis quartus is very large, its ventral fibres blend with the pectoralis major, and its dorsal fibres with the latissimus dorsi, while it is covered superficially by the panniculus: here evidently the muscle is derived from the same sheet as the pectoralis major and latissimus; it fills the entire interval between the two, and, remembering that it is covered on its surface by the panniculus, we must consider that this condition militates strongly against the idea that the quartus is panniculus. (2) In two cases of Dr Brooks the achselbogen was attached to the pectoralis quartus instead of to the lower border of the great pectoral: here the quartus evidently took the place of part of the major. This also favours Professor Owen's view. And, lastly, the condition which is found in the Cat would seem to show that it is apparently impossible that the pectoralis quartus could be derived from the panniculus. In this animal, except with great care, it is very difficult to accurately separate the panniculus from the underlying muscles, particularly from the axillary borders of the pectoralis major and latissimus dorsi; but if it be first raised on the dorsal aspect of the trunk, and then carefully dissected towards the axilla, the

[1] The subcutaneous thoracic branch of the brachial plexus of Chauveau, who also recognises in it the representative of the nerve of Wrisberg.

[2] *Jour. Anat.*, July 1887.

following condition of parts will be found:—The axillary interval is very narrow, in one place the pectoralis major and latissimus actually touch; lying in this narrow interval, and under cover of the adjacent part of the pectoralis major to a considerable extent, we find the pectoralis quartus,[1] while the panniculus covers the interval and its contained muscle completely. Converging towards the axilla, its dorsal fibres are rather closely united to the axillary border of the latissimus; the most anterior of these pass forwards to be inserted into the humerus, the more posterior fibres cross the axilla, *passing obliquely* over the pectoralis quartus, and end partly by blending with the axillary border of the great pectoral, partly by passing over this border and becoming lost on the outer surface of the muscle; indeed, the panniculus in this animal might be described as a muscular sheet passing from the outer surface of the latissimus dorsi obliquely, or almost transversely across the axilla to the outer surface of the great pectoral, and shutting off the axilla and its contents from all superficial structures, its fibres crossing those of the pectoralis quartus very obliquely. Here, again, we have a condition of parts which seems to preclude all possibility of the pectoralis quartus having been derived from the panniculus; so it would appear most probable that Professor Owen's theory is the correct one—that the pectoralis quartus is a segmented portion of the great pectoral muscle.

As regards the achselbogen, I shall begin by discussing those views which appear least probable, and most easily examined.

First, Mr Galton's idea that the achselbogen corresponds to the pectoralis quartus. This view has been disposed of in connection with the pectoralis quartus.

Mr J. B. Perrin's view that the slip in question is an aborted variety of dorso-epitrochlearis, is scarcely more tenable. The dorso-epitrochlearis agrees with the achselbogen in none of our criteria except in origin—both spring from the latissimus at the junction of muscle and tendon; in position and insertion there is absolutely no resemblance, and in nerve-supply there is the widest difference, the dorso-epitrochlearis, as pointed out when speaking of the pectoralis quartus, is supplied by a branch

[1] Where the pectoral and latissimus meet, the quartus is *completely overlapped by them.*

of the musculo-spinal nerve, the achselbogen is normally supplied by a branch of the internal anterior thoracic, as will be shown later on. Further, Mr J. T. Wilson [1] records two cases of achselbogen in the human subject, and in each of these a dorso-epitrochlearis was present as a separate and distinct muscle. Evidently we can find no grounds for considering achselbogen and dorso-epitrochlearis the same; and we pass on to the consideration of the other views.

Of the two remaining theories regarding the nature of the achselbogen,—Professor Humphry's, that it is due to an imperfect segmentation of pectoral from latissimus, and Sir William Turner's, that it is panniculus,—each seems so probable, and when tested by the different criteria gives such proof in support of its claims for adoption, that we can decide which is probably the correct one only after a careful and thorough investigation of both. If the achselbogen were really formed, in the manner suggested by Professor Humphry, by the imperfect separation of the latissimus from the pectoral muscles, if it were simply a connecting band left after the incomplete splitting of one layer of muscle into two parts, we should expect to find the connecting slip passing from the *margin* of one division very obliquely across the interval to the margin of the other. Apparently the achselbogen fulfils these conditions; at first sight it seems to spring from the axillary edge of the latissimus, where its fibres look as if they were perfectly continuous with the fibres of that muscle, indeed, it would seem as if a band of the substance of the latissimus had been bent across the axilla to the opposite border, where it blends with the pectoralis major; still, if we examine the attachment of the achselbogen to the latissimus, or what we may call the origin of the slip, we will find that in the majority of cases the connection between the two is not what it seems to be upon casual inspection. I have dissected with great care a few of these attachments, and I have found that the achselbogen instead of springing from the very edge of the muscles, does not actually do so; traced backwards it passes over the margin, crossing the fibres of the latissimus *obliquely*, and becoming attached to its outer surface some distance from the edge. Secondly, the muscular fibres of the latissimus *seem*

[1] *Jour. Anat.*, January 1888.

to pass uninterruptedly into those of the achselbogen. On dissection, I have found this not to be so; the little muscle followed backwards over the margin of the latissimus passes into a thin flat aponeurotic band, and the other end of this band blends with the muscular substance on the back of the latissimus. (Luschka[1] considers that this little aponeurotic band described above is always present when the achselbogen springs from the muscular part of the latissimus; Testut[2] is not convinced of its constant presence.) Then we have found (1) that the fibres of the achselbogen cross obliquely those of the latissimus dorsi; (2) that they do not spring from the margin of the muscle; and (3) that they are not continued into the fibres of the latissimus, but end in an aponeurotic band which is attached to the outer surface of that muscle. All these facts militate against Professor Humphry's view, and, as I shall point out afterwards, favour the claims of the panniculus. In position and insertion the achselbogen fulfils the conditions laid down above, as those that should be present in a muscle formed according to the imperfect segmentation theory. Let us now apply our last criterion, nerve-supply: if the achselbogen be derived from the imperfect separation of the pectoralis major and latissimus, it ought to participate in the nature of one of these muscles, as well as in that of the other,—consequently its nerve-supply ought to be double, it should be derived from the nerve to its pectoral, as well as from that to its dorsal parent. Do we find such a nerve-supply for the achselbogen? I may answer at once—no. But before proceeding any further it would be well to decide what is the normal nerve-supply of the muscle in question.

In the January number of the *Journal of Anatomy* for 1888 Mr J. T. Wilson, in an interesting account of the dissection of two cases of achselbogen, records the nerve-supply. On one side he found it came from the intercosto-humeral, the lateral cutaneous of the third intercostal piercing the muscle; on the other side, it was innervated by a branch from the nerve of Wrisberg, which in this case sprang from the inner cord of the brachial plexus by a trunk common to itself and the internal anterior thoracic.

To Professor Cunningham I am indebted for the notes of two cases read by him before the British Association in Montreal,

[1] Testut on *Muscular Anomalies*, p. 111. [2] *Ibid.*

1884; in both the nerve came from the internal anterior thoracic, and the intercosto-humeral pierced the muscle without supplying it.

Karl Bardeleben[1] records a case where the nerve came from the internal thoracic also.

Dr Brooks has kindly sent me notes of two cases which he met,—in one the nerve came from the internal thoracic, in the other, from the loop of communication between the two thoracics; the intercosto-humeral pierced the muscle in one of these cases.

I myself have twice found the nerve,—once it arose from the inner cord of the brachial plexus, between the internal thoracic and the nerve of Wrisberg; in the other case, it came from the internal thoracic after it had received the usual communication from the external, but the fibres were traced into the trunk of the internal above the connection; an extremely minute twig of the intercosto-humeral entered 'and was lost in the muscle, this I considered simply a sensory filament.

Thus we find that, out of nine cases, in five the nerve to the achselbogen came directly from the internal anterior thoracic, in one case from the loop between the inner and outer anterior thoracics, in one from the inner cord close to the origin of the internal thoracic, and in one from the nerve of Wrisberg, which arose by a trunk common to it and the internal anterior thoracic; the nerve in these three latter cases, although differing superficially from the condition in the first five, is probably fundamentally the same in origin; so that out of the nine we have only one which really differs from the others, namely, that of Mr Wilson, in which the nerve came from the intercosto-humeral; this exception, I think, we must consider an abnormality. I have never found upon direct stimulation of the nerve that the intercosto-humeral contained motor fibres.[2] From the foregoing I may safely, I think, draw the conclusion that the achselbogen is normally supplied by the internal anterior thoracic nerve. And further, as far as I can find, there has not been recorded a case in which the subscapular nerve supplied a branch to the achselbogen; such a branch I have looked for with great care, but always with negative results.

[1] *Jen. Zeitschrift für Naturwissenschaft*, Bd. xv. N. F. viii., 1881.

[2] In animals.

Then in nerve-supply we see that the achselbogen differs from the condition which we should expect to find if that muscle were really derived from the imperfect separation of the latissimus dorsi from the pectoralis major; if such were its true nature it should have not only a nerve from the internal thoracic, but also one from the long subscapular, indeed we might expect to find this latter the chief nerve of the muscle, seeing that it is most closely connected with the latissimus. The fact that I could find no branch from the subscapular to the achselbogen first shook my belief in the theory of Professor Humphry, which I held as most probable when I began this inquiry; the result was that I turned to the view of Sir William Turner, with what fruits I shall now proceed to show.

Professor Turner considered the achselbogen—as well as several other muscular slips, which he described in the first volume of the *Journal of Anatomy*—a derivative of the panniculus. My investigation of the subject leads me to the same conclusion, namely, that the achselbogen is a derivative of the anterior and dorsal portion of the humeral panniculus.

In animals we generally find the humeral panniculus as a thin sheet converging from the lateral region of the trunk towards the axilla, where it is inserted in connection with the pectoralis major, on its deep surface as a rule; its ventral fibres overlie the great pectoral, the dorsal fibres cover the latissimus, and the intermediate fibres lie against the lateral thoracic wall. From the anterior dorsal fibres I believe the achselbogen is derived; coming from the back, they sweep over the latissimus dorsi across its axillary margin, and then run obliquely over the axillary interval to their insertion in connection with the pectoralis major. From this it will be seen that in position and insertion this portion of the panniculus agrees exactly with the achselbogen, and indeed in a carefully dissected humeral panniculus one is struck immediately by the resemblance which its anterior border bears to an axillary muscular arch—notably in position. Then, tested by two criteria, position and insertion, panniculus and achselbogen correspond. Now, as regards origin, or what we have decided to consider origin, namely, attachment to the latissimus dorsi, is it possible that a portion of the panniculus could come to be so intimately connected to the

latissimus as the achselbogen commonly is? The answer is—Yes. If we examine the panniculus in several animals we shall find every step in the change from panniculus passing freely over the axillary border of the latissimus to the condition of the achselbogen, where the union between the two is so intimate that one seems to be merely a slip of the other. In most animals, *e.g.*, Rabbit, Horse, Macaque, &c., the dorsal portion of panniculus passes as a somewhat thickened border freely over the latissimus to its insertion, as described above. Next, in the Cat we find it rather closely adherent to the latissimus at its margin. In the *Cynocephalus anubis*, Mr Champneys,[1] speaking of the panniculus, says:—"It gave a few fibres to the latissimus dorsi after having previously received a few from it." Here, evidently, are two steps towards the condition at the origin of the achselbogen. Dr A. MacCormick,[2] after describing the pectoralis quartus in *Phalangista vulpina*, says:—"The lower part of its tendon is joined by a slip from the latissimus dorsi, and the slip contains fibres from the panniculus carnosus as well as fibres from the latissimus itself." Lastly, Mr Galton[3] writes:—In the Wombat "a slip is moreover sent from the interior part of the latissimus dorsi over the axillary vessels and nerves to join the highest part of the tendon of the pectoralis major." This, he says, "may belong, however, to the panniculus carnosus; but this latter is so closely blent with the anterior edge of the latissimus dorsi that it is difficult to satisfactorily see the nature of the muscle in question." Here we have the panniculus and latissimus so closely united at the axillary border that they cannot be distinguished from one another—a close approach to the condition of the achselbogen at its origin from the latissimus; indeed, another step brings us to the achselbogen itself. This apparently close connection between latissimus and achselbogen is on the surface the greatest obstacle to Sir William Turner's view that the latter muscle is panniculus; so close is the union between them that it is almost impossible to

[1] *Jour. Anat.*, vol. vi. p. 177. He remarks that the connection between the panniculus and latissimus seems to be represented occasionally (Henle and Wood) in man by a connection between latissimus dorsi and pectoralis major, *i.e.*, by achselbogen.

[2] *Jour. Anat.*, Oct. 1886.

[3] *Trans. Linn. Soc.*, vol. xxi.

get rid of the idea that the achselbogen is some way or another derived from the latissimus dorsi. But the obstacle is not insurmountable if we remember, as I have already pointed out, that the fibres of the achselbogen are not directly continuous with those of the latissimus, but are simply attached to the back of that muscle through the medium of an aponeurotic band; and, secondly, that the panniculus, as shown above, may become so closely blended with the latissimus that the two are practically inseparable.

A few other points in connection with the blending of the two muscles. Professor Humphry, in his *Observations in Myology*,[1] describes the panniculus as a superficial stratum of the ventral muscle segmented off from the "external oblique layer." He further tells us that this segmentation is often incomplete, and that the two layers are more or less blended at places; when this is so, the junction of the segmented with the unsegmented portion of the superficial layer is effected through the medium of fibrous septa—such a blending and such a junction we apparently have at the origin of the achselbogen from the latissimus dorsi. We may consider the achselbogen as panniculus which is segmented off from the deeper parts in the region of the axilla, unsegmented over the latissimus, and the union between the two parts is effected through the medium of the little aponeurotic band which I have already described as attaching the achselbogen to the back of the latissimus. This condition of the achselbogen agrees in every detail with Professor Humphry's observations about the panniculus above quoted.

Again, Professor Turner[2] describes an axillary muscular arch receiving a number of scattered fasciculi which arose from the superficial aspect of the fascia over the serratus magnus, and along with these were other fasciculi which were attached to the fascia forming the floor of the axilla. Here apparently we have the remains not only of the anterior dorsal portion of the panniculus—as in the ordinary achselbogen—but also a trace of the portion which covers the lateral aspect of the thorax. Even more of the sheet has been found by the same anatomist[3] in a

[1] Pp. 109 and 129.

[2] *Jour. Anat.*, vol. i. p. 252, *footnote*. [3] *Ibid.*

well-marked bundle springing from the pectoral fascia turning round the axillary border of the pectoralis major and forming the achselbogen. And a somewhat similar slip is described by Professor Humphry.[1]

I need go no further to show that the panniculus, not only in position and insertion, but also in its connection with the latissimus dorsi, can present a condition exactly similar to that of the achselbogen, and three of our criteria are satisfied. Next let us apply the test of nerve-supply to the panniculus and achselbogen.

The achselbogen, I have shown above, is normally supplied by the internal anterior thoracic nerve; the nerve-supply of the panniculus certainly seems very different, in animals it is supplied by a nerve known as the "lateral cutaneous nerve of the thorax," or the "subcutaneous thoracic branch of the brachial plexus." We shall examine this nerve. In his able paper on the limb plexuses in mammals, Dr A. M. Paterson[2] describes it in the Porcupine, which is taken as a typical mammal. Here part of the ventral division of the eighth cervical joins a branch of the first thoracic to form the lateral cutaneous nerve of the thorax, which runs down the side of the trunk under cover of the panniculus, supplying it and the skin of the axilla, and communicating with the lateral cutaneous branches of the intercostal nerves. In this lateral cutaneous of the thorax Dr Paterson recognises the homologue of the nerve of Wrisberg—which is otherwise generally absent in mammals—and he bases this opinion on its origin, on its distribution to the skin of the axilla, and on its communicating with lateral cutaneous branches of the intercostal nerves. Dr Paterson's idea of the homology of the nerve under consideration is supported by Mr J. T. Wilson in the *Journal of Anatomy* for January 1888. Chauveau[3] also states that the lesser internal cutaneous (nerve of Wrisberg) is represented in quadruped by the subcutaneous thoracic (lateral cutaneous of thorax).

That the lateral cutaneous of the thorax which supplies the panniculus represents the nerve of Wrisberg to a large extent

[1] *Observations in Myology*, p. 131, *footnote*.
[2] *Jour. Anat.*, July 1887.
[3] Chauveau's *Compar. Anat.* by Fleming, p. 768.

is probably correct, but at the same time I believe that it represents not only the nerve of Wrisberg, but, in addition, part, or sometimes the whole, of another nerve.

If Dr Paterson's view be true, then the panniculus is supplied by the nerve of Wrisberg, the achselbogen by the internal anterior thoracic, and, tested by the most important of the four criteria, Professor Turner's theory fails. But, on the other hand, if we can show that the lateral cutaneous of the thorax contains within it other fibres than those representing the nerve of Wrisberg, then there is still hope for the view that achselbogen is panniculus. To aid us in arriving at the true nature of the nerve, we shall examine it in a series of animals.

I have already pointed out that the pectoralis quartus is supplied by a branch of the internal anterior thoracic nerve, and I think I am correct in saying that such is its nerve-supply in every animal that has an internal thoracic (considering the fact that the quartus is undoubtedly a member of the pectoral group, it would naturally be supplied by a pectoral or anterior thoracic nerve). Now, in the Opposum, Kangaroo, and Wallaby[1] the pectoralis quartus is supplied by the lateral cutaneous of the thorax; the internal thoracic is absent, and the external sends the branch of communication which usually passes between the two thoracics to the lateral cutaneous of the thorax instead. These are significant facts. Why does the lateral cutaneous supply the pectoralis quartus? Why does it receive the communication from the external thoracic? The answer must be, because it contains embodied within it the internal anterior thoracic in addition to the representative of the nerve of Wrisberg. This is the only conclusion we can arrive at after a consideration of the above facts; and as we examine a series of animals we shall find other grounds for this conclusion, we shall find every step between the condition in marsupials where the two nerves are united into one, and the condition which obtains in man where the two are distinct and separate.

In the Rabbit I found a nerve springing from the trunk formed by the last cervical and first thoracic, this nerve divided into internal thoracic and lateral cutaneous of thorax; in other words, the two nerves arose by a common trunk.

[1] Mr Wilson, *loc. cit.*

In the Cat, which, like other Carnivora, is said to want a pectoralis minor, I met the following arrangement:—Two thoracic nerves arose from the trunk formed by the seventh cervical alone, these were both distributed to the great pectoral; the posterior or inner of the two sent a communicating filament to the next branch described, this branch arose by two roots from eighth cervical and first dorsal. These roots united received the communication referred to above from the thoracic, and then divided into two parts; one of these went to the pectoralis quartus, the other was the lateral cutaneous of the thorax.

In the Dog I found the lateral cutaneous formed by two roots of nearly equal size; one came from the posterior (inner) cord of the brachial plexus, the other from the internal anterior thoracic. In this animal the constitution of the lateral cutaneous is evident; we see plainly that it is made up largely of fibres of the internal thoracic,—these are probably the motor fibres for the panniculus,—and in addition of fibres derived from the posterior cord (inner), which may probably be sensory only, and represent the nerve of Wrisberg. So far we have in the marsupials described, the two nerves completely united: in the Rabbit the two united for a short distance, in the Dog the internal thoracic furnishing half the fibres of the lateral cutaneous, and a somewhat similar condition in the Cat. From this it is clear that the two nerves—internal thoracic and lateral cutaneous—are most intimately connected both in origin and distribution; and, further, that the lateral cutaneous probably always contains a large number of fibres from the internal thoracic trunk. Moreover, it appears that fibres may sometimes come with apparent indifference from either one or the other of these nerves. For instance, in the Hedge-Hog I have seen the internal thoracic and the lateral cutaneous arise side by side from the posterior or inner cord of the plexus; the internal thoracic was distributed to the pectoralis minor as usual, the lateral cutaneous to the panniculus. The latter nerve was very large, and a short distance from its origin it gave a small branch to the pectoralis minor, that is, a pectoral branch arises from the lateral cutaneous. I have found the opposite condition in the Horse; in this animal a large nerve arose from the trunk formed by the first and second thoracic nerves, this divided into the lateral cutaneous

(subcutaneous thoracic) and large branches to the so-called posterior deep pectoral; from one of these branches to the pectoral came a nerve which was distributed to the panniculus; on stimulation I found that this branch, as well as the lateral cutaneous, contained motor fibres for the panniculus. Here we find a pectoral nerve giving off a branch which should have come from the lateral cutaneous. These two cases afford further evidence of the close connection existing between the two nerves.

But in the Macaque Monkey I have found the link required to connect the condition of the lateral cutaneous of the thorax in the mammals described above with that found in man. In this animal the internal anterior thoracic, which arose from the inner cord of the brachial plexus, gave off a branch which divided into two parts; one of these went directly to the pectoralis quartus, the other was joined by a branch of the intercosto-humeral, and then divided immediately into the nerve to the panniculus and a nerve which corresponded in distribution to the nerve of Wrisburg in the human subject.[1] Here at last we have the divorce of the two constituents of the lateral cutaneous from one another, and the key to the true nerve-supply of the panniculus. Let us examine the arrangement more closely. A branch from the intercosto-humeral—*ergo*, from the second dorsal nerve—joins with a comparatively large branch of the internal thoracic. Now, if they remained joined, and ran down to the panniculus, they would have formed a lateral cutaneous exactly similar to the same nerve in the Rabbit (previously described); and we would describe the condition by saying that the lateral cutaneous and the internal thoracic arose by a common trunk, that lower down the lateral cutaneous communicated with the intercosto-humeral—like the lateral cutaneous in other animals—and that it was then distributed to the panniculus. The same terms will apply to the lateral cutaneous in the Rabbit. But in the Macaque, instead of remaining one single nerve, a division takes place—a separation of the two parts which would form a lateral cutaneous similar to that of the Rabbit and other mammals—and as a result we have a nerve

[1] This condition is not constant in the Macaque, but I have found it three or four times.

of Wrisberg corresponding in distribution to the human one, and a nerve to the panniculus. And this nerve of Wrisberg is not only similar in distribution to the nerve of the same name in man, but is similar, to a certain extent, in origin too, for most of its fibres are derived from the intercosto-humeral branch of the second dorsal nerve; and it seems very probable that the nerve of Wrisberg derives some of its fibres from the second dorsal, through the communication usually found connecting it with the first, the majority of the fibres coming from the first dorsal. Owen says the nerve of Wrisberg is formed by fibres derived from the eighth cervical and first dorsal, but I have never been able to trace fibres of the cervical nerve into it.[1] On the other hand, I have found it receiving a considerable contribution from the second dorsal—indeed, the alternation in size found between this nerve of Wrisberg and the intercosto-humeral prepares one for the fact that the second dorsal usually contributes to the formation of the lesser internal cutaneous. (Further, in this connection I have found the nerve of Wrisberg absent as a branch of the brachial plexus in man, and its place completely filled by a lateral cutaneous branch of the first intercostal, which arose from the trunk soon after the nerve came out from the intervertebral canal, but pierced the intercostals in the axillary line. Here the representative of the nerve of Wrisberg could not possibly have received fibres from the eighth cervical, and the condition of the nerves, when taken with other considerations, leads one to the idea that the nerve of Wrisberg is the lateral cutaneous branch of the first intercostal nerve to a large extent.[2]) Now, we will naturally inquire, where does the nerve to the panniculus in the Macaque get its motor fibres? It must be from one or both of those nerves which, by their union in this animal, give rise to the nerve to the panniculus and the nerve corresponding to the lesser internal cutaneous. These

[1] Mr Herringham (*Proc. Roy. Soc.*, p. 431, Nov. 30, 1886) says the nerve of Wrisberg was formed by the first dorsal (in which he includes the communicating twig from the second) in nineteen out of twenty cases examined by him; in one case a filament came from the eighth cervical.

[2] According to Owen (*Comp. Anat.*) the lateral cutaneous branch of the third intercostal, and according to Swan (*Comp. Anat.*, "Nerv. System") the lateral cutaneous of the second intercostal corresponds in the Fox to the nerve of Wrisberg.

are the intercosto-humeral and the internal anterior thoracic. I have already stated that, by stimulation of the intercosto-humeral (in several animals), I could never make the panniculus contract; further, in most animals the intercosto-humeral pierces the panniculus without giving any fibres to it—a relation similar to that in Professor Cunningham's, and one of Dr Brooks', cases of achselbogen recorded above; and lastly, the lateral branches of the intercostal nerves are cutaneous or sensory. Considering these facts, we must infer that the intercosto-humeral does not supply the motor fibres to the panniculus, and we arrive at the conclusion that it is supplied by the internal anterior thoracic. This nerve is, I believe, the true motor nerve of the panniculus.

Dr Paterson's opinion that the lateral cutaneous nerve of the thorax is the homologue of the nerve of Wrisberg seems strange, in view of the facts that the nerve of Wrisberg is entirely a sensory nerve and the lateral cutaneous is chiefly motor, for its sensory fibres are very few, and seem to be derived chiefly from communications with the lateral cutaneous nerves of the thorax. An examination of the nerve in the marsupials mentioned in the Dog and the Macaque point directly to the fact that it is a compound nerve, formed by the union of the homologue of the nerve of Wrisberg with part of the internal thoracic, or with the whole of that nerve in some marsupials.[1] I may add that the internal thoracic and the nerve of Wrisberg, in the human subject, occasionally spring by a common trunk from the inner cord of the plexus; and, even when they spring separately, if the plexus be teased out, it will often be found that they unite within the cord to form a distinct bundle, so that, even in man, the close connection between the two nerves is apparent.

Returning, then, after a long digression, to the achselbogen, we found that the panniculus agreed with it in origin, position, and insertion. We are now able to add that it agrees with it in nerve-supply too, and all our criteria are satisfied. So we may conclude that Professor Sir William Turner's theory, tested by the criteria proposed, is the true one, namely, that the

[1] And, seeing that the nerve is chiefly motor, the "nerve to the panniculus" would seem a more appropriate name than the "lateral cutaneous of the thorax," unless we substitute musculo-cutaneous for the term cutaneous alone.

achselbogen is derived from the humeral part of the panniculus carnosus.

In the foregoing I think I have adduced sufficient proof to show (1) that the pectoralis quartus is a segmented portion of the great pectoral; (2) that the achselbogen is a derivative of the panniculus; (3) that the pectoralis quartus is supplied by the internal anterior thoracic nerve; (4) that the achselbogen is supplied by the same nerve; and lastly, that the lateral cutaneous nerve of the thorax is the homologue of the nerve of Wrisberg, associated with more or less of the internal thoracic; or, perhaps, it might be more correctly put, that the lateral cutaneous of the thorax is the homologue of (*a*) the nerve of Wrisberg, associated with (*b*) another nerve which usually arises, and is closely connected, with the internal thoracic. This second nerve (*b*) I consider a distinct element, which increases or diminishes with the panniculus, and which is absent in man, as a rule, but is occasionally represented as the nerve of the achselbogen.

OBSERVATIONS ON THE EARLIER STAGES IN THE DEVELOPMENT OF THE LUNGS OF RATS AND MICE. By ARTHUR ROBINSON, M.B., C.M., *Senior Demonstrator of Anatomy, Owens College, Manchester.* (PLATE XII.)

THE origin of the hypoblastic portion of the lung-substance from the walls of the fore-gut has been definitely established in several mammals,[1] but comparatively little attention has been paid to the manner in which the epithelial bronchi increase; and, with the exception of His,[2] no one has compared the embryological appearances with those which Aeby's[3] extensive researches have pointed out as being characteristic of the adult lung.

There can, however, be no doubt that the embryological history of the bronchial tubes, as Aeby himself has observed, will throw much light upon the adult condition, and the knowledge of this history, in a series of mammals, will serve either to confute or confirm Aeby's opinions, which are based entirely upon the careful examination of a large series of adult lungs. It is from this point of view that the following observations have been made.

Observations on Embryos.—In sections taken transversely to the long axis of embryo rats, about five days old, the fore-gut, at the level of the posterior aortic arches, has the appearance of a transverse slit, having a dorsal and a ventral wall. In the middle line of the ventral wall there is a slight bay-shaped depression, and a similar, though slighter depression, exists in the middle line of the dorsal wall. At this time the heart is doubled upon itself, and the bay-shaped depression in the ventral wall of the pharynx is placed in the mesoblast of the mesentery, immediately dorsal to the auricle. The epithelium forming the wall of the pharynx is thick ventrally and at each lateral angle, but dorsally it consists, at this level, of a single

[1] Rathke, *Ueber die Entwicklung der Athmungswerkzeuge bei den Vögeln und Säugethieren;* Bischoff, *Entwicklungs des Menschen und der Höheren Thiere;* Kölliker, *Entwicklungsgeschichte des Hundesies;* Coste, *Histoire générale et particulière du developpement des Corps organisés.*

[2] His, "Zur Bildungs-geschichte der Lungen beim menschlichen Embryo," *Archiv für Anat. u. Phys. Anat. Abtheil*, 1887.

[3] *Der Bronchialbaum der Säugethiere und des Menschen*, Leipsig, 1880.

layer of somewhat cubical cells, which have a greater vertical height in the middle line than laterally.

In this position the ventral wall of the fore-gut may be considered as consisting of two lateral portions, separated by the bay-shaped depression before noted; and each half has its long axis directed from side to side. As the fore-gut passes backwards, each lateral half of the ventral wall gradually changes its position until its long axis is directed dorso-ventrally. In this manner a groove is produced in the ventral wall of the fore-gut, it is shallow anteriorly and deep posteriorly, being deepest immediately in front of the opening of the gut into the umbilical sac. Further, behind the auricles, the ventral end of the furrow thus produced is laterally expanded, and the greatest expansion is on the right side (fig. 1). The ventral furrow is the rudiment of the trachea, and the lateral expansions at its posterior end are the first representations of the bronchial tubes.

Whilst the ventral wall of the fore-gut, as it passes from before backwards, thus alters its shape, the dorsal wall also undergoes a change of form. Just behind the level of the posterior aortic arches it consists, like the ventral wall, of two lateral halves, directed from side to side, and separated by a shallow mesial depression. As the gut is traced backwards, each lateral half is seen to become gradually more and more oblique, being directed from above down and out, whilst at the same time it diminishes in extent. It follows, from the varying positions of the walls of the fore-gut at different levels, that, in the region of its lower end, the pharynx has, in transverse section, the appearance of a cross, the horizontal limb of which is much longer than the vertical.

Farther back the appearance, in transverse section, is that of a quadrilateral space, having a dorsal and two lateral angles; and still farther posteriorly, in consequence of the elongation of the ventral angle of the quadrilateral space and the lateral expansion of the ventral end, the transverse section of the fore-gut becomes somewhat dumb-bell-shaped (fig. 1).

It has been already stated that the epithelium of the ventral wall of the gut at the lower end of the pharynx is thicker than that on the dorsal wall; this arrangement of the cells is the same throughout the whole length of the tube, and they are

specially thickened in the region of the lateral expansions at the posterior end of the ventral furrow.

The mesoblast surrounding the epithelial tube is scanty, and consists dorsally of stellate cells, whilst laterally and ventrally the cells are more rounded, and appear to be due to proliferation of the cellular lining of the body-cavity and of the splanchnic mesoblast surrounding the vitelline veins.

On the sixth day the bay-shaped depression in the ventral wall of the posterior end of the pharynx is more distinct than in the preceding stage, whilst farther back the dorsal section of the fore-gut is more rounded. The ventral furrow is comparatively deeper, and the lateral expansions at the posterior part of the furrow are larger, but there is as yet no separation of the ventral from the dorsal section of the gut. The mesoblast surrounding the epithelial tubes is considerably increased in amount, but laterally and ventrally the cells still retain the uniformly rounded appearance.

During the next two days a great advance is made. Sagittal sections of eight-day embryos show that the ventral furrow is becoming separated, by the rapidly increasing mesoblast, from the dorsal portion of the fore-gut. The separation commences behind and passes forwards till the whole of the ventral furrow is cut off, except in front, where, in the region of the future glottis, it still remains connected with the dorsal portion of the gut.

At the same time, the ends of the lateral expansion from the termination of the primitive trachea project themselves outwards and backwards into surrounding mesoblast, which proliferates rapidly, and form two bud-like projections into the body-cavity, one on each side the middle line, dorsal to the auricles. The formation of the primitive bronchi is due to the backward growth of the lateral expansion of the trachea, and not to splitting of the posterior end of the trachea by ingrowing mesoblast.

Sections of the bronchi at this stage show them to be circular tubes uniformly but slightly expanded at their blind posterior terminations. The cells of the mesoblast still retain their rounded character, even where they are placed between the rudiments of the trachea and œsophagus, but they have begun to mass themselves more closely round each epithelial tube.

During the next day the epithelial bronchial tubes continue their backward growth and gradually lose their original uniform

roundness, whilst at the same time each epithelial bronchus acquires special characters of its own. Thus on the right side the tube is at first circular in transverse section, then triangular, the deepest angle projecting dorso-externally; farther back the tube is again circular, and it terminates in a uniformly expanded extremity. The formations which give rise to these appearances have been produced either by partial constriction of the terminal enlargement of the preceding stage into two unequal parts, and the subsequent more rapid growth of the inner and larger portion, or the production of an expansion in the outer wall of the tube. The sections of this stage in my possession do not suffice to decide between the two methods, but examination of older embryos indicates that the first is the one adopted. The terminal, expanded, and more rapidly-growing portion becomes the continuation of the stem bronchus, whilst the lateral projection is the first rudiment of the most anterior branch on the right side. On the left side, transverse sections of the anterior part of the epithelial bronchus are circular in outline, farther back oval, and the termination of the tube is, as on the right side, uniformly expanded; there is no clear indication of the formation of any secondary branch from this tube. The round mesoblastic cells have increased, and are thickly massed round the trachea and round the œsophagus also, having extended backwards in the mesentery to the dorsal surface of the latter tube.

The growth now proceeds still more rapidly, and during the next three days the terminal portion of the right epithelial bronchus is three times divided, and the terminal portion of the left twice, so that on the thirteenth day four hollow buds project from the wall of the right epithelial bronchus, three from the outer side of the main stem, and one from its ventral surface. The latter is placed between the second and third side branches.[1] On the left side there are only two hollow buds from the main epithelial tube, both from its outer side. During the thirteenth and fourteenth days the terminal portion of each principal epithelial tube is again subdivided, whilst the bud-like outgrowths from the main stems have increased in size. The surrounding mesoblast

[1] In the following account the first branch from the right bronchus, "eparterial bronchus," is classed as a lateral branch, because, at its commencement, it springs more from the lateral than from the posterior surface of the right-stem bronchus.

has shared in the rapid vegetative activity which characterises the growth of the epithelial tubes, and on the fifteenth day each lung is represented by an elongated ridge of mesoblast, rounded at its anterior and posterior extremities, projecting from the mesentery of the fore-gut into the dorsal section of the anterior portion of the body-cavity, the ventral part of the anterior portion of the body-cavity having been cut off, in a manner which will be afterwards described, to form the pericardium. Each mesoblastic ridge has in transverse section a triangular outline (figs. 2–4). The angles are dorsal, external, and internal; the latter corresponds to the attached margin of the lung. The surfaces between the angles are dorsal, lateral, and ventral. The main stem of the epithelial bronchial tree runs in the attached border of the mesoblastic ridge, and the branches given off at this stage are directed towards the lateral angle.[1] There is, moreover, a notch in the outer surface of the right lung germ which indicates the future separation of the lung into an anterior and a posterior portion, and a bud-like projection from its ventral surface, near the attached border, is the rudiment of the azygos lobe (fig. 4).

The first branch given off from the right-stem bronchus rises from the outer surface of the tube, and is directed dorso-laterally (fig. 2, *Bl.* 1). It is given off immediately above the point at which the right pulmonary artery, which is now distinguishable, crosses the ventral surface of the main epithelial tube. At its origin from the main stem it is circular and comparatively narrow, but it rapidly enlarges, forming a globular expansion in the anterior portion of the mesoblastic ridge. The second branch also rises from the outer surface of the main bronchus, but behind the point at which the latter is crossed by the pulmonary artery (fig. 3, *Bl.* 2). The third branch is projected from the ventral surface of the stem bronchus ventrally and internally, into the bud-like projection which eventually becomes the azygos lobe (fig. 4, *Br.* 1).

The fourth and fifth branches are given off from the outer surface of the main tube, the fourth is a circular bud, and the

[1] The "lateral branches" in this description correspond to the "ventral side bronchi," the dorsal branches to the "dorsal side bronchi," the "ventral" to the "ventral accessory," and the "dorso-internal" to the "dorsal accessory" of Aeby's nomenclature.

fifth is not yet completely separated from the main tube (fig. 5, *Bl.* 3 and *Bl.* 4). The branches from the left stem bronchus all arise behind the point at which the latter is crossed by the pulmonary artery; they originate from the outer surface of the stem and are all directed laterally. At this time the right lung is longer than the left, it is also broader and thicker, and its bronchi are more numerous and larger. His states that in the human being the branches on the left side are most developed.[1] The pulmonary arteries rise separately from the aortic bulb; they run outwards and backwards, and cross ventrally to the corresponding bronchi. Afterwards, continuing their backward course, they lie on the outer side of main epithelial tube, and dorsal to the branches given off from its lateral surface. On the right side the pulmonary artery, as it crosses to the outer side of the main tube, passes between the first and second lateral branches. On the left side the artery crosses to the outer side in front of the first branch from the stem bronchus.

Coronal sections of rat embryos at this stage indicate clearly the method of production of the lateral branches (fig. 5). They are evidently due to flattening of the terminal expansion opposite the axis of the tube, and subsequent division of the expansion into two unequal portions, of which the larger becomes the continuation of the stem, and the smaller becomes the lateral branch. The mesoblast cells immediately surrounding the epithelial bronchi have become elongated, and the tubes are thus surrounded by two or three layers of spindle-shaped cells. The arrangement of the mesoblast round the œsophagus is somewhat different; the cells lying next to the epithelium are elongated parallel to the tube, whilst those more externally placed form two or three concentric circles of spindle-shaped cells, arranged round the long axis of the œsophagus.

Development proceeds rapidly on the lines already indicated. The mesoblast increases in amount, the main epithelial tubes elongate and produce many offshoots, which in their turn become extensively ramified, and on the nineteenth day each lung appears in transverse section still more distinctly triangular; but the surface which was previously ventral or ventro-external is now, in the middle portion of the lung, directed ventrally and

[1] *Loc. cit.*, p. 99.

internally, the change of position being, in great part, due to the rapid increase of the mesoblast at the outer angle (figs. 8, 9). The separation of the right lung into its permanent lobes is accomplished. Two fissures pass obliquely inwards from the lateral surface, separating the lung substance into an anterior portion, chiefly dorsal, a middle, and a posterior portion, whilst the azygos lobe has extended from right to left across the middle line of the body, and lies between the œsophagus and left lung above, and the heart below (fig. 9).

The right main bronchus gives off fourteen branches, of which the first only is placed anterior to the pulmonary artery. Thirteen are placed behind the pulmonary artery; of these five are directed laterally, two pass ventrally and internally, and of the remaining six, which were unrepresented in the stages previously described, four project dorsally from the main tube, and two dorsally and internally. The left bronchus gives eleven branches, all posterior to the crossing of the pulmonary artery, five lateral, four dorsal, and two open dorsally and internally. The dorsal branches rise from the main stem internal to the pulmonary artery, which is therefore situated on the outer side of the stem between the dorsal and lateral branches (figs. 8 and 9). The dorso-internal branches rise from the main stem close to, and on the inner side of, the dorsal branches (fig. 9).

Tabular View of the Branches from each Stem Bronchus on the Nineteenth Day.

Left Bronchus.	*Right Bronchus.*
1. Lateral, behind pulmonary artery.	1. Lateral, in front of pulmonary artery.
2. Dorsal.	2. Lateral, behind pulmonary artery.
3. Lateral.	3. Ventral.
4. Dorsal.	4. Dorsal.
5. Dorso-internal.	5. Lateral.
6. Lateral.	6. Dorsal.
7. Dorsal.	7. Dorso-internal.
8. Dorso-internal.	8. Lateral.
9. Lateral.	9. Dorsal.
10. Dorsal.	10. Dorso-internal.
11. Lateral.	11. Lateral.
	12. Dorsal.
	13. Lateral.
	14. Ventral.

The arrangement of the mesoblast is similar to that found on the fifteenth day, except that the inner layer of cells round the œsophagus has increased in thickness.

On the fifteenth day there is no trace of the dorsal and dorso-internal branches; they arise between the fifteenth and nineteenth days, and are associated in their development. On the right side the first dorsal branch is situated on the main stem between the first ventral and the third lateral branches, whilst in the human lung His[1] figures the first dorsal branch as rising from the stem above the ventral branch. My sections of human embryos confirm the correctness of this position. The origin of the second dorsal branch on the right side is placed between the second and third lateral branches. On the left side the first dorsal branch is between the first and second lateral branches, and the second dorsal between the second and third lateral (fig. 7). The dorso-internal branches are closely connected with the dorsal branches. An examination of the first dorsal branches on the left side shows that the hollow bud becomes flattened opposite its point of origin (fig. 8). This flattening is followed by a constriction which separates the bud into internal and external portions. The second dorsal branch immediately after its origin is similarly divided, and the constriction passes rapidly towards the axial stem, until its apex reaches the level of the circumference of the main bronchus (fig. 9). Thus, from the dorsal bud, a dorsal and a dorso-internal branch are formed. They rise close together from the main stem, but never on exactly the same level, for the constriction which separates them passes obliquely, so that the orifice of the dorsal branch is placed partly on a level with, and partly above, that of the dorso-internal, or *vice versâ*.

The rate of growth, both of the epithelial tubes and the surrounding mesoblast, is now increased, and between the nineteenth and twenty-fourth days the number of branches given off from the right stem bronchus advances from fourteen to twenty-five, and from the left to main bronchus from eleven to twenty-two. During the same time the main stems have themselves increased in length, and those primary branches which were first produced are now richly ramified. The increase of

[1] *Loc. cit.*, pl. vii. fig. 15.

the number of branches from the stem bronchi has been produced not only by repeated division of the terminal portion of each main bronchus, but also by the appearance of hollow outgrowths from the stem. For example, on the nineteenth day only one dorsal and one dorso-internal branch intervened between the third and fourth lateral branches from the left stem bronchus, but on the twenty-fourth day there are two dorsal and two dorso-internal branches between the third and fourth lateral bronchi; it is perfectly clear that of these one dorsal and one dorso-internal must have been produced as hollow buds from the wall of the stem bronchus. But whilst, on the one hand, the number of branches rising from a certain portion of the stem bronchus has been increased by the formation of bud-like outgrowths from the wall of the latter, and by the rapid growth of the septum, which divides dorsal buds into dorsal and dorso-internal branches, it has been decreased, on the other hand, by comparative diminution of the rate of growth of the septum separating the orifices of origin of dorsal from dorso-internal branches. Thus, on the nineteenth day, the sixth branch from the right main bronchus is dorsal, and the seventh, which is almost on the same level as the sixth, is dorso-internal, but on the twenty-fourth day both these branches rise from a single short trunk, so that the number of branches rising from this portion of the stem has been reduced by one.

Little or no change has taken place in the mesoblast cells immediately surrounding the trachea and bronchi. They are spindle-shaped, and are arranged circularly round the epithelial tubes, but do not appear to have increased in number. The remainder of the mesoblast, however, has altered its character; its cells are more loosely arranged, and more irregular in form.

As the character of the growth by which the main bronchi and their branches increase in extent and ramification as to the period of birth does not differ from that already indicated, any description of the further stages would be but useless repetition, and it is only necessary therefore to consider as briefly as possible the branches given off from the main bronchi.

The first lateral branch from the right stem bronchus is represented on the ninth day by a bulbous expansion on the wall of the stem bronchus. It grows rapidly, and on the

fifteenth day is attached to the parent stem by a distinct hollow stalk, and the expansion is flattened opposite the axis of its stalk. Between the fifteenth and nineteenth days the expansion is divided into two parts—a lateral, which is continued outwards and forwards towards the apex of the lung, and a posterior, which passes backwards and outwards. The ramification is explained by the subjoined tabular statement:—

First right lateral branch = Eparterial Bronchus	lateral	dorsal	anterior.
			posterior.
		lateral	dorsal.
			lateral.
	posterior	dorsal	dorsal.
			posterior.
		lateral	dorsal.
			lateral.

This bronchus and its branches occupy the most anterior lobe of the right lung.

The second lateral branch from the right stem passes outwards into the middle lobe of the lung, and on the nineteenth day gives off four branches, of which the first two and the fourth are dorsal, and the third ventral.

The third lateral branch from the right bronchus is the fourth branch to appear, but on the nineteenth day it is the fifth branch on the stem. It is directed outwards and slightly backwards, and gives off four branches, the first and third being ventral branches, the second and fourth dorsal.

The fourth lateral bronchus is the eighth branch from the right stem on the nineteenth day; it gives off at this time two subdivisions, of which the first is dorsal, the second ventral.

The remaining lateral branches from the right stem bronchus on the nineteenth day are the eleventh and thirteenth branches. The former is a hollow-stalked bud, and the latter merely a bay-like evagination from the wall of the stem bronchus.

Five lateral branches are found on the stem of the left bronchial tree on the nineteenth day. The first three of these were the first branches given off from the stem, but as the result of the formation of dorsal and dorso-internal branches between the fifteenth and nineteenth days, at the last named

period the second lateral bronchus is the third branch from the stem, and the third lateral bronchus is the sixth branch.

All the branches of the left stem bronchus rise behind the point at which the latter is crossed by the pulmonary artery.

The following description of the lateral branches of the left stem bronchus refers to the appearance they present on the nineteenth day.

The first lateral branch, immediately after its origin, divides into two almost equal portions, of which one passes forwards and outwards towards the apex of the lung, and the other is directed ventrally and outwards. The further subdivision is indicated in the following tabular arrangement:—

- First lateral branch of left bronchus
  - anterior
    - dorsal
      - anterior
      - posterior
    - lateral
      - anterior to anterior end of lobe
      - lateral
        - dorsal
        - ventral
  - posterior
    - ventral
    - lateral
      - dorsal
      - lateral
        - anterior
        - lateral

The second lateral branch passes outwards and gives three branches—the first and third are ventral, the second dorsal.

The third lateral bronchus has two branches—the first a ventral, the second a dorsal.

The fourth lateral branch is, at this period, simply an undivided saccular dilatation.

The dorsal and dorso-internal branches on the right side are all enclosed in the posterior division of the lung. On the left side the lung is undivided, and the position of the dorsal and dorso-internal branches is sufficiently indicated by the tabular statement on page 230.

On the right side the ventral branches, with the exception of the first, which is distributed to the azygos lobe, are included in the posterior division of the lung. On the left side these branches are of comparatively late development, not appearing until after the twenty-fourth day.

Remarks.—In the rat and mouse, as in the guinea-pig,[1] rabbit,[2] and man,[3] the epithelial part of the respiratory organs is first formed as a groove in the ventral wall of the fore-gut. In the rat and mouse this groove extends from the region of the last pair of aortic arches to the opening of the fore-gut into the umbilical sac. The opening into the umbilical sac is placed immediately behind the heart, and is separated from the latter organ by a layer of mesoblast, formed by the union of the splanchnic and somatic layers, which meet at this place (fig. 10). From this point of union a mesoblastic septum extends forward and dorsally to the anterior end of the body-cavity, which it divides into a ventro-anterior portion, the pericardium, and a dorso-posterior part—the pleuro-peritoneal cavity (fig. 11). The septum contains the vitelline veins and the ducts of Cuvier, and gives origin, eventually, to the walls of the pericardial sac and the ventral half of the central portion of the diaphragm. The statements made regarding it are so contradictory, and the terms used so confusing, that it may be well to take a short survey of its formation.

In its primitive condition the heart is double, and consists, on each side of the body, of a simple dilatation on a vessel which lies in the splanchnic mesoblast. This vessel behind the heart is termed the vitelline vein, and in front of the heart it is called the aorta. During the next stage the splanchnic mesoblast is rapidly infolded, both laterally and antero-posteriorly. In the anterior portion of the embryo this infolding takes place along the line of the vessels, and, proceeding rapidly, cuts off the dorsal portion of the hypoblastic cavity, which retains the form of a transverse slit. Beneath this slit, which is the pharynx, the dilated portions of the vessels meet and fuse, giving rise to the single median heart. More posteriorly the infolding of the splanchnic mesoblast is not so rapid, and the folds meet ventral to the level at which the vitelline veins are situated (fig. 11). The vertical height of the fore-gut is, as a result, greater, and, as the mesoblastic cells on each side of the epithelial tube rapidly increase, the tube itself becomes laterally compressed.

Whilst the above changes are proceeding, the infolding of the somatic walls has taken place both from the sides and from the

[1] Rathke, *loc. cit.* [2] Kölliker, *loc. cit.* [3] His, *loc. cit.*

ends, and consequently as the vertical depth of the fore-gut increases, from its anterior end to its connection with the umbilical sac, its ventral wall, surrounded by splanchnic mesoblasts, gradually approaches the somatic wall, and eventually they meet at the umbilical orifice, at which point the somatic and splanchnic mesoblasts fuse (fig. 10).

The fusion of the two layers takes place only in front of the umbilical orifice, and not laterally nor posteriorly. It results, therefore, that, at this point, a transverse septum of mesoblastic tissue is formed in the middle line of the body, and through this septum the vitelline veins pass to reach the sides of the mesentery of the fore-gut. Other changes have been proceeding coincidently with those already described, and, especially, the mesoblast on the outer sides of the vitelline veins has proliferated rapidly, and has extended from the veins to the lateral walls of the body (fig. 11), and thus, as the veins pass from behind forward and upward, rising dorsally as the mesentery of the fore-gut diminishes in height (fig. 10), a transverse septum is formed on each side of the mesentery of the fore-gut, extending from the vitelline vein to the lateral wall, and from the umbilical orifice forward and dorsally to the anterior end of the body-cavity.

The ventral part of the anterior division of the body-cavity is cut off and forms the pericardium, whilst the dorsal part of the anterior division of the body-cavity, which finally forms to two pleural sacs, is divided by the mesentery of the fore-gut into two halves (fig. 11), each of which communicates posteriorly with the peritoneal cavity. The mesoblastic septum, which separates the pericardial sac from the remainder of the body-cavity, contains anteriorly the ducts of Cuvier, and from it are produced the parietal pericardium, the pericardial pleura, and at its posterior and ventral end, where the splanchnic and somatic layer of mesoblast are fused, it is the precursor of part of the parietal pericardium, the ventral half of the central portion of the diaphragm, and of the liver and its peritoneal covering.

The dorsal portion of the central part of the diaphragm is developed from the mesoblast surrounding the fore-gut at the level of the anterior border of the umbilical orifice. The lateral portions of the diaphragm are formed as outgrowths from the

body walls. Commencing at first in front, in the region of the transverse mesoblastic septum, they extend dorsally and inwards towards the middle line, and gradually shut off the pleural from the peritoneal portions of the body-cavity.

It is while the changes which result in the formation of the pericardium are proceeding that the walls of the ventral section of the fore-gut, immediately in front of the umbilical sac and dorsal to the pericardium, bulge out, first on the right side and then on the left, so that two vesicular projections are formed which open widely into the ventral section of the fore-gut, an arrangement of parts corresponding exactly with that found by Kölliker[1] in the rabbit. The two vesicular projections have been already described as the rudiments of the bronchial tubes, and their rapid growth and division gives rise to the numerous bronchi of the adult lung.

The method of division by which the richly ramified bronchial tree of the adult is produced has been differently described by several observers.

Aeby,[2] whose statements are based upon the examination of the lungs of a large series of adult animals, says that a main stem is produced, from which two series of branches are given off, a dorsal and a ventral; and this opinion is supported by Kölliker,[3] who states that on the twelfth day in the rabbit the first branches are given off dorsally and laterally. More recently, His,[4] describing the development of the human lung, points out that the first branches are given off from a main stem, but the stem afterwards divides dichotomously, and the ramification of the lateral branches is the result of a similar dichotomy. Stieda,[5] appears to consider that ramification results from repeated division of the original germ, whilst Küttner[6] strongly insists on the terminal increase of the stem, and the origin of the branches as sprouts given off at right angles from it.

In the rat and the mouse the ramification of the bronchi is produced principally by dichotomy. The germ of each bronchus, as it grows outwards and dorsally, becomes expanded at its ter-

[1] *Loc. cit.*, p. 858.
[2] *Loc. cit.*, p. 859.
[3] *Loc. cit.*
[4] *Loc. cit.*
[5] *Zeitsch. f. wiss. Zool.*, Bd. xx.; Suppl. Bd., s. 108.
[6] "Studien über das Lungenepithel," Virchow's *Archiv*, lxvi. p. 13, 1876.

mination; this expansion is gradually constricted into two portions of unequal size, that is the dichotomy is the form described by the botanist as unequal or sympodial. The larger division becomes the stem, and the smaller has the appearance of a branch, which in its turn becomes divided in a similar manner. This is well seen in fig. 5.

In the account given by His[1] of the development of the human lungs he states that, after the formation of the first bronchus, the new branches are produced only from the end knobs. This is not the case in the rat and mouse, for, although most of the branches are produced by dichotomous division of terminal expansions, certain of the dorsal branches arise as hollow buds from the wall of the stem bronchus after it has assumed its cylindrical form, and these buds are interpolated between pre-existant branches.

Before proceeding to a consideration of the signification of the various branches, it is necessary to summarise Aeby's opinions concerning them.

Aeby states that each bronchial tree forms a monopodial system, the main stem of which increases by terminal growth, and gives off branches from its sides. The pulmonary artery, as it crosses the stem bronchus, from within outwards, is taken as the boundary line between two sets of branches. The branches in front of the artery are eparterial; those behind it hyparterial. The hyparterial branches form two groups. In one group the branches are directed dorsally, in the other ventrally,[2] and the pulmonary artery, as it passes backwards along the outer face of the main stem, lies between the dorsal and ventral branches. Aeby has further pointed out that other branches may rise from the inner side of the stem bronchus, and these, on account of their generally smaller size and less importance, are called accessory branches; he suggests that, originally belonging to either the dorsal or ventral branches, near which they lie, they have been transferred to the stem branches. He terms them, according to their position, dorsal or ventral accessory branches.

[1] *Loc. cit.*, p. 101.

[2] Originally these branches are placed laterally, and have been spoken of in the preceding description as "lateral branches." At a later period they are directed ventrally, on account of the rapid growth of the outer angle of the lung.

To one of the accessory branches—the first ventral—Aeby draws special attention, pointing it out as the branch situated in the azygos or infracardiac lobe, which is so generally found in mammals.

There can be no doubt that the primary branches from the main stem, behind the pulmonary artery, are the lateral and dorsal. On this point, Kölliker's observations on the rabbit, those of His on the development of the human lung, and my own on the lungs of rats and mice, support Aeby's opinion.

Regarding the dorsal accessory bronchi, His makes no statement. In rats and mice they are always produced from the primary dorsal expansions, whether those have arisen by division of the terminal portion of the stem bronchus or as hollow buds from the walls of the latter. In no case have I been able to find a dorsal accessory (dorso-internal branch) originating by division of the terminal portion of the stem bronchus or as a hollow bud from its wall.

The development of these branches in rats and mice is, therefore, entirely confirmative of Aeby's suppositions regarding them.

The case of the ventral accessory bronchus is not so clear. His has shown that in the human lung the branch which Aeby looks upon as the first ventral accessory bronchus has a distinct and separate origin from the main stems, and he concludes that it is therefore equal in value to the other primary branches.[1] In the rat and mouse it is the third branch, produced on the right side (fig. 4) by the division of the terminal portion of the stem bronchus. At no time has it any connection with the first ventral hyparterial branch. It increases in size more rapidly than many of the primary lateral branches. Elsewhere it has been pointed out[2] that examination of this bronchus in the adult lung indicates that in some animals its separate position, its large size, and its method of ramification, give it a value quite equal to that of the primary lateral branches. But, although the developmental history of this branch in man and the rat, and its peculiar relations in many adult lungs, show

[1] "Für seine Selbständigheit spricht fernerhin sein frühes Auftreten und die weite Entfernung, welche ihn sowohl vom ersten als vom zweiten ventralen Bronchus trennt," *loc. cit.*, p. 99.

[2] Young and Robinson, *Jour. Anat. and Phys.*, Oct. 1888.

that, ontogenetically, it must be considered as a primary subdivision of the main stem, still, observations carried out on a series of adult lungs demonstrate that, phylogenetically, the branch is, as Aeby suggests, originally a subdivision of the first lateral hyparterial bronchus.

Eparterial Branches.—Aeby has shown that, as a rule, only one branch is given off from the stem bronchus in front of the covering of the pulmonary artery. This branch may be absent on one or both sides, but when present it always supplies the most anterior portion of the lung. He suggests, that if it is present on the right side and absent on the left, the portion of lung supplied by it is also absent on the left side. In the rat and mouse there is an eparterial bronchus on the right side. It originates at the first division of the bronchial germ, and constitutes the first branch from the stem; its ramification has already been indicated. As a distinct branch it is absent on the left side, but it is compensated for by the first lateral hyparterial branch, which divides, immediately after its origin, into two parts, one of which, totally unrepresented on the corresponding bronchus of the right side, runs forward to the apex of the lung; therefore the first left ventral hyparterial branch must be considered as, to a certain extent, corresponding to the eparterial and the first ventral hyparterial bronchi of the right side. This arrangement corresponds with that found by His in the human lung.

EXPLANATION OF PLATE XII.

A, aorta.
Ae, œsophagus.
Au, auricle.
B, stem bronchus.
Bd, dorsal branch of stem bronchus.
Bl, lateral branch of stem bronchus.
Bv, ventral branch of stem bronchus.
(*Bd*, *Bl*, *Bv*: Numbered 1, 2, 3, &c., according to order of appearance.)
F, fore-gut.
L, left side.
La, anterior lobe of right lung.
Lm, middle „ „
Lp, posterior „ „
Lz, azygos „ „
Omp, vitelline vein.
P, pericardium.
Pa, pulmonary artery.
Pl, pleural sac.
R, right side.
S, spinal cord.
Tr, trachea.
V, ventricle.

The outlines of all the figures, except 10 *and* 11, *were drawn with the camera lucida* (*Zeiss objective* AA *and ocular No.* 2). *Figures* 10 *and* 11 *are diagrammatic.*

Fig. 1. Transverse section of an embryo five days old, showing the germ of the right bronchus; the commencement of the left bronchus is seen as a very slight evagination on the left side of the fore-gut of the embryo.

Figs. 2, 3, 4, 5, and 6 represent sections of embryos of the same age (about fourteen days). They show the relative positions of the various branches and the position of the pulmonary artery. Figs. 2, 3, and 4 are transverse vertical sections of the lungs. Fig. 5 is a coronal section. Fig. 6, a sagittal section.

Figs. 7, 8, and 9 represent sections of the lungs of embryos about nineteen days old. They indicate the relative positions of the branches of the stem bronchi at that period, including the dorsal and dorso-internal branches, which have appeared between the fifteenth and nineteenth days.

Figs. 8 and 9 are vertical transverse sections. Fig. 7, a sagittal section.

Fig. 10 shows the relation of the ventral wall of the fore-gut to the body wall at the fifth day, and indicates the point at which the splanchnic and somatic mesoblast fuse in front of the umbilical orifice. The dark line which represents the hypoblast indicates the level at which the vitelline veins pass forward to reach the auricles, *e.g.*, the level of the transverse septum, which divides the pericardium from the body-cavity.

Fig. 11 represents a transverse vertical section at the level of the line *R* in fig. 10. It shows the division of the body-cavity into two parts by the transverse septum which contains the vitelline veins.

ON HEXADACTYLISM, WITH ESPECIAL REFERENCE TO THE SIGNIFICATION OF ITS OCCURRENCE IN A VARIETY OF THE *GALLUS DOMESTICUS*.

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IN vol. xx. p. 93, of the *Journal of Anatomy and Physiology*, I have described the pentadactylous foot as it occurs in the Dorking variety of the common fowl. Occasionally, however, there occurs in the same variety a hexadactylous condition. One of the Dorkings figured by Tegetmeier, in his work on poultry, is that of a male bird possessing six toes, but in the text the possession of a sixth toe is referred to as undesirable.

The following is the description of the feet of an old male bird presenting this peculiarity, and which I recently dissected:—In the recent condition the feet presented six distinct toes, all perfectly separate from each other, and freely movable on the foot. The plantar aspect of all the toes was worn, as if by coming in contact with the ground. The toe most superior and internal in position cannot, however, have been of much, if any, functional value in walking.

Regarding the osteology of the feet, the tarso-metatarsus in the specimen under consideration does not materially differ from the corresponding bone in the pentadactylous specimen—that is, it is divided inferiorly into three articular surfaces, as it is in most other birds. There is thrown out from the shaft of the tarso-metatarsus, on its inner and posterior aspect, an osseous process, or roughened tuberosity of bone, which has projecting from it the osseous core of the spur.

On the inner side of the right foot there is a somewhat flattened, irregularly cuboidal bone, which is ligamentously attached to the inner side of the tarso-metatarsus, immediately above the innermost of the three articular surfaces just referred to (fig. p. 249). On its dorsal aspect there is a longitudinal groove, which divides its inferior extremity into two articular surfaces, with which surfaces the proximal phalanges of two digits articulate. This bone apparently corresponds to the rudimentary metatarsal bone in the pentadactylous pes already alluded to, and

to the same bone present in the foot of most other birds, though absent in many of the Grallæ and aquatic birds. It is also absent in the Ratitæ, with the exception of the apteryx, in which this innermost digit is represented by two small segments.

In the left foot the arrangement of this bone is somewhat different; there it is completely fused with the tarso-metatarsus, occupying the same relative position as it does as a separate bone in the right foot. Its line of fusion is clearly indicated by a ridge of bone both on the anterior and posterior aspect of the tarso-metatarsus, and also by a well-marked notch separating its inferior articular process from the tarso-metatarsus. It possesses, like the corresponding bone in the right foot, two articular surfaces for articulation with two digits.

Between the tuberosity above referred to, as present on the inner side of the shaft of the tarso-metatarsus and the rudimentary metatarsal bone, there is present a digit composed of three segments, the proximal one of which articulates with a slight prominence on the tarso-metatarsus just above the rudimentary metatarsal bone. This digit has the proximal and middle segments on the left foot anchylosed, while the middle and distal phalanges of the corresponding toe on the right foot are in a similar condition.

Next in order come two digits, each possessing two phalanges, the proximal phalanx of each articulating respectively with the superior and inferior articular facets on the distal extremity of the rudimentary metatarsal. Then follow the three digits usually present in the foot of birds, and possessing respectively, from within outwards, 3, 4, and 5 phalanges, and articulating as usual with the three articular processes present on the lower end of the tarso-metatarsus (fig. p. 249).

In other respects the various phalanges of the six digits are of normal formation, and are freely movable at their respective articulations. The terminal phalanx of all the digits bears a claw. In these hexadactylous feet I believe that the four outer digits, possessing respectively, from within outwards, 2, 3, 4, and 5 phalanges, correspond to the four outer digits of the pentadactylous feet already alluded to, and to the four toes of an ordinary tetradactylous bird.

These cases of polydactylism have arisen, as it seems to me,

in one of two ways, viz., either as monstrosities or as cases of reversion by arrest of development. If the hexadactylous pes be assigned to the former, then there seems no reason why the pentadactylous form should not also be disposed of in the same way; but if they are regarded as monstrous formations, then they are peculiar in being so hereditary. Would it not be remarkable for a monstrous formation to be so truly transmitted as to become an essential characteristic of a certain breed of animals, as is the case with the pentadactylous Dorking fowl?

Certainly Mr Bland Sutton has advanced the view that certain constant structures may have had a pathological origin, such, for instance, as the warts on the inner side of horses' legs. If, on the other hand, these cases be referred to arrest of development, then the rudimentary metatarsal represents, as I previously stated with reference to the pentadactylous foot, the elements of the 1st and 2nd metatarsals. In such a case they should probably be regarded as cases of reversion to a primitive vertebrate form, possessing six digits on the pes. The existence of a six-toed vertebrate is not a mere supposition, for in the *American Journal of Science*, vol. xix., February 1880, there is a paper by Professor O. C. Marsh, on "The Limbs of Sauranodon, with notice of a new species." From this paper it seems that there have now been described nine specimens, belonging to two distinct species of the genus Sauranodon. The specimen here alluded to is from the secondary formations, having been found in a series of marine deposits—named by Professor Marsh the Sauranodon beds—in the Upper Jurassic of Wyoming.

This genus is of especial interest in possessing an extremely generalised anterior and posterior extremity. According to Professor Marsh, the limbs were used as paddles for swimming, and are less specialised than those of any other vertebrate above the fishes. In the fore paddle the humerus alone is differentiated, and the radius perhaps partially so. There are six metacarpals and six distinct digits. "In the posterior limb the structure is essentially the same." That is, there are six metatarsals and six digits, each consisting of several rounded undifferentiated phalanges. The same authority also states—"The six complete digits in the limbs of Sauranodon is a character not before

observed in any air-breathing vertebrate. Some of the amphibians retain remnants of a sixth digit, and Ichthyosaurus often has outside the phalanges one or more rows of marginal ossicles that evidently represent lost digits. With these exceptions, the normal number of five digits is not exceeded."

I am aware that in the text-books on Comparative Anatomy and Zoology it is stated that in birds it is digit V. (minimus) which has disappeared, and that the metatarsal corresponding to this outer digit has become fused with the distal tarsal element, which latter is in turn fused with the metatarsus to form the tarso-metatarsus. In a paper "On the Tarsus of Birds," Dr G. Baur [1] says that he, like Rosenberg, had suggested that metatarsal V. disappears during the course of development in birds, but that more recent researches of his show that metatarsal V. does not disappear, but blends with the second row of the tarsus. In the fowl, he says, that takes place between the eleventh and fourteenth day. This latter points clearly to the existence of an extra toe on the fibular side of the foot in birds.

There however remains the fact, that there is the remnant of an extra toe on the tibial side in many five-toed amphibians, in reptiles, and in a large number of mammals. The evidence of this latter is quite clear, as the following statements show:—

Bardeleben,[2] in a paper "On the Morphology of the Bones of the Hand and Foot," says:—"There exists a rudiment of an inner (tibial) toe from the hallux, a tarsal or metatarsal of the prehallux or O. in Monotremes, in American Marsupials, Edentata, Carnivora, Rodents, Insectivora, and Monkeys."

Wiedersheim states, in his *Comparative Anatomy of Vertebrates*, pp. 104 and 105, that the amphibians possess five complete digits on the posterior extremity, and traces of an extra toe are also seen on the tibial side of the tarsus.

The following passage occurs in Darwin's *Animals and Plants under Domestication*, p. 458:—"Six toes have been described on the hind feet of the newt (*Salamandra cristata*), and are said to have occurred with the frog. It deserves notice that the six-toed newt, though adult, preserved some of its larval

[1] *Zoologischen Anzeiger*, No. 202, 1885.

[2] *Sitzungsberichten der Jenaischen Gesellschaft für Medicin und Naturwissenschaft. Jahrg.*, 1885.

characters, for part of the hyoidal apparatus, which is properly absorbed during the act of metamorphosis, was retained."

Wiedersheim also states in the work just quoted, on p. 109:—"In human embryos of the second month a distinct cartilage is present on the tibial side of the tarsus, and this probably answers to a small bone on the tibial border of the foot of Monotremes, American Marsupials, Edentates, Carnivores, Rodents, Insectivores, and Monkeys. This most likely corresponds to an extra (first) toe ('prehallux,' Bardeleben)." In the Reports of the Challenger Expedition,[1] Sir William Turner, when dealing with the anatomy of the seals, has figured the bones of the foot of *Arctocephalus australis*, in which there occurs an extra bone in the tarsus. Its position is internal to the scaphoid and entocuneiform, and the aforesaid anatomist has named this bone the entoscaphoid.

Professor Turner has also called my attention to the fact that there exists a similar bone in the foot of *Eumetopias cinereus*. In a skeleton of the sea lion (*Otaria jubata*), in the Edinburgh Museum of Science and Art, the entoscaphoid is an elongated bone, occupying a position internal to the scaphoid and entocuneiform. Possibly this bone is the tarsal remains of a "prehallux."

Baur and Albrecht[2] regard this tibial sesamoid bone present in many mammals as tibiale. Gegenbaur,[3] on the other hand, regards the astragalus as consisting of *tibiale* and intermedium, as does also Bardeleben on embryological grounds.

Bardeleben[4] speaks of a bone on the inner side of the tarsus of the Virginian opossum, which he provisionally considers as a rudimentary sixth toe. In regard to this, Baur, in the paper just alluded to, says:—"I can completely confirm Bardeleben's view. In *Didelphys virginia* (young 5·15 mm.) I find the 6th toe of the tarsus consisting of two distinct pieces of cartilage." "We have also found in the carpus and in the tarsus of mam-

[1] Part lxviii. vol. xxvi., "Zoology."

[2] *Zoologischen Anzeiger*, No. 196, 1885, "On the Morphology of the Carpus and Tarsus of Vertebrates."

[3] *Untersuchungen zur vergleich. Anatomie der Wirbelthiere*, Heft. 1, "Carpus and Tarsus," Leipzig, 1864, p. 121.

[4] "Zur Entwicklung der Fuszwurzel," *Sitzungsber. Jena. Gesellschaft Jahrg.*, 1885.

mals, rudiments of a radial relatively tibial toe." "The sesamoid bone of the abductor pollicis is the last remains of the digit in the hand; the supernumerary pieces of bone, which by de Blainville in his *Osteography* are represented in the tarsus of many beasts of prey, belong to the last remains of this toe in the foot." The Dog frequently possesses five digits on the pes, the innermost toe being a rudimentary or extra toe consisting of *three* osseous segments. More rarely there are present six digits on the pes of large dogs, the two innermost being rudimentary. There is, therefore, sufficient evidence to show that pentadactylous vertebrates have, more or less completely lost a digit from the tibial side of the pes.

In the hexadactylous foot of the bird which I have described above, I believe that the hallux is there represented by the digit second in position from the spur. Whether the innermost digit represents another lost digit, viz., the "prehallux" of other vertebrates alluded to above, I am not at present prepared to say, for to do so would be to presuppose the existence of a primitive vertebrate possessing seven digits. No such creature is at present known to palæontologists, unless the marginal ossicles of Ichthyosaurus be regarded as indicating such a condition. If my interpretation of these birds' feet be correct, then, as I stated in my previous article in this *Journal*, the present enumeration of the digits on a bird's pes is incorrect. That is to say, in order that the enumeration of the digits of an ordinary tetradactylous bird correspond to the enumeration in other vertebrates, they should be numbered from within outwards, not I., II., III., and IV., but II., III., IV., and V., as indicated in the diagram, p. 249. As polydactylism has received most attention in the human subject, I will briefly refer to it as occurring in man. M. Gaillard, quoted by Mr Annandale, in his *Diseases of the Fingers and Toes*, p. 26, divides supernumerary digits in the human subject into three varieties:—

"1st. The finger is only bifid, articulating with the metacarpus by a single head."

"2nd. Two fingers are placed in juxtaposition, being articulated side by side, only one articular capsule surrounding the head of the metacarpal bone."

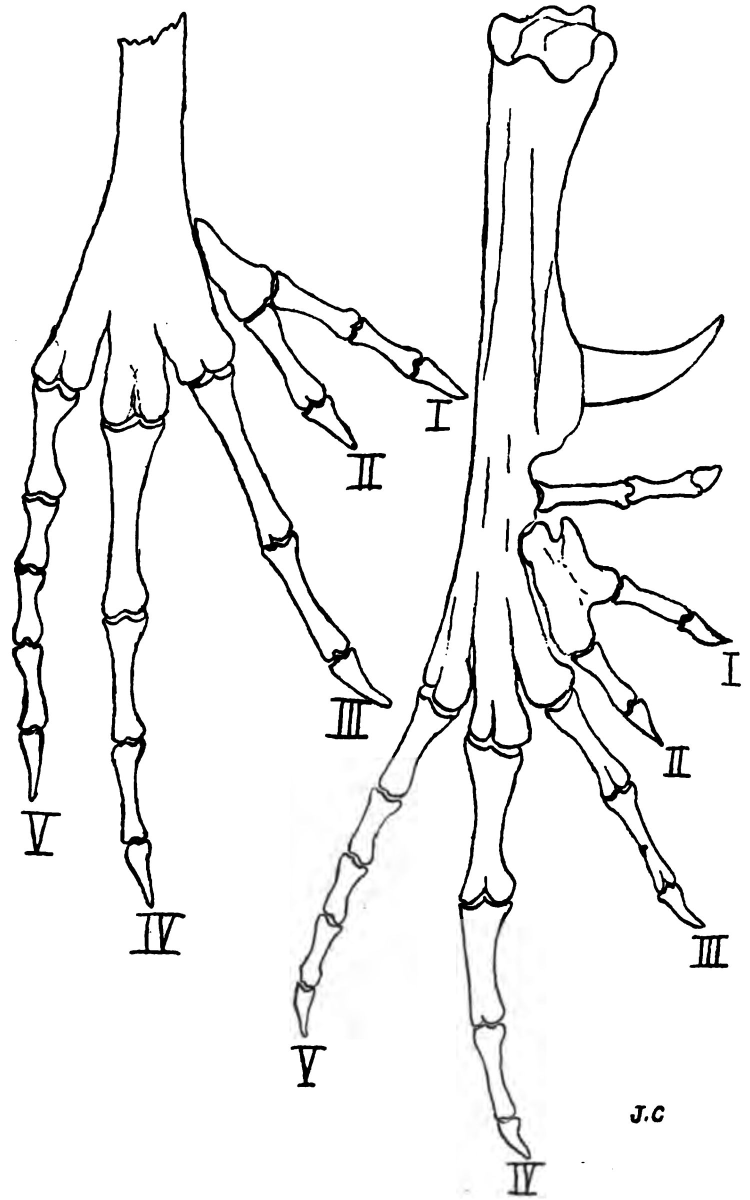
"3rd (rarest). The supernumerary finger is entirely isolated,

and implanted on a special articular surface of the metacarpus, the superfluous part almost always being a thumb or great toe."

It is also stated by Mr Annandale that "fingers and toes are most commonly increased in number by one only, but cases are on record in which this number has been greater." Indeed, the various cases on record show that the number of digits normally present may be exceeded by very varying numbers till we reach, so far as I am aware, a maximum in the following case, mentioned by Darwin in the *Descent of Man*, p. 37:—"I am informed by Dr Zouteveen, that there is a case on record of a man having twenty-four fingers and twenty-four toes." This was most probably a case of duplication of both hands and feet, or perhaps merely the fingers and toes; if it was an example of the former, which is rarer, it is interesting in presenting four hexadactylous hands and feet.

Considering the cases figured and described by Mr Annandale, and from an examination of cases of polydactylism under his care in the Edinburgh Royal Infirmary last winter, and also of a number of casts of this condition in the Anatomical Museum of the University of Edinburgh, I may say that the cases possessing several supernumerary digits, present the appearance of more than one hand or foot incompletely separated; that is, they are what are commonly called monstrous formations.

But in the vast majority of cases of polydactylism, there is only one extra digit present, and this is perfect in structure and external appearance. After eliminating the cases which are due to partial or complete duplicity of limbs, and judging from the foregoing facts presented by amphibians, reptiles, birds, and mammals, bearing upon the question of hexadactylism, it seems possible to look upon the condition occurring in man, as well as in other vertebrates, as a case of reversion to a hexadactylous form.


I
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THE CONSTRUCTION OF THE VENTRICLES IN THE MAMMALIAN HEART. By Macdonald Brown, M.B., F.R.C.S., *Lecturer on Anatomy at Surgeons' Hall, Edinburgh.*

Some doubt still exists as to the precise method in which the interventricular septum of the mammalian heart is formed, as to how much of it is due to an inflection of the anterior common wall of the ventricles, or to the growth of a special internal septum.

But however formed, once perfect it divides the ventricular chamber into two cavities of nearly similar capacity, whose walls are practically of equal thickness. By the rapid growth of the body of the fœtus, the left cavity is soon called upon to exercise much greater muscular power than the right, its walls therefore thicken much more than those of the latter cavity, until they reach the ordinary proportions of 3 to 1. The septum grows at a similar rate, and eventually becomes of the same thickness as the remainder of the left ventricular wall.

The thin-walled right ventricle is meanwhile somewhat stretched by the rapid growth and thickening of the left, and there is thus presented on transverse section the well-known appearance where the left ventricle is a thick-walled circle, the right a crescent. The right ventricle consists apparently only of a single wall, crescentic on section, and attached to the cylindrical left cavity along the interventricular line. The blood is expelled from the left chamber by the contraction of its own walls, while the right expels its blood mainly by compressing it from below upwards against the convex septum.

Pettigrew, in his paper on the "Structure of the Heart," implies that the right ventricle, on account of its construction and relations, is an "accessory" one. With this opinion I do not agree.

Through the kindness of Sir William Turner, I have lately had opportunity of investigating thoroughly the Heart Collection in the Anatomical Museum of the University of Edin-

burgh. Throughout the entire series of the Mammalia there represented, the right ventricle is large and well formed, and although in most mammals, just as in Man, the separation between the two cavities is poorly marked on the external aspect, in two cases, at least the external separation is distinct, viz., in the Dugong, where the ventricles are separated from each other in the lower half by a large gap, and in less degree in the heart of the Porpoise, where a well-marked interventricular groove exists, much deeper than that found in the ordinary Mammalian heart, and specially marked anteriorly, and near the apex. My attention was first directed to the grooved condition of the heart of the Porpoise by Sir William Turner.

If, to regard the right ventricle, on account of its anatomical configuration, as an accessory or secondary one be (as I believe) erroneous, then physiologically it seems a still greater mistake to speak of it as such, considering that its function is equal in importance to that of its fellow ventricle.

With reference to the trabeculæ carneæ which are present generally in both cavities, opinion is divided. Most anatomists regard them as meaningless, and merely an incidental developmental occurrence. Certainly, on examining such a heart as that of the Serpent, where they not only exist as a network all over the internal surface of the ventricles, but also form the imperfect and cribriform septum, they appear merely to represent a developmental stage. It seems to me, however, that their very presence (more especially in bridge form) must aid largely in effecting the complete emptying of the blood from the chambers, and also to some extent in counteracting any tendency to over-distension in the lower half of the cavity.

My own observations on the subject apply solely to the right ventricle. On opening the right ventricle of the human heart by flap incision, there can be made out two papillary muscles, named from their relative position, anterior and posterior.

In the series of 100 hearts examined, I found the anterior muscle large, well formed, and very definite in position. Attached near the cardiac apex, to about the middle of the crescentic wall, its base, in the great majority of cases, begins in a radiation of trabeculæ, many of which are of bridge form. Its origin therefore affects a large area of the free ventricular wall. Its

chordæ are distributed to the two parts of the larger segment of the tricuspid valve in the manner so well known.

The posterior muscle is much smaller, is irregular in position, is frequently replaced by two or more smaller ones, and in some cases is absent altogether. The few chordæ attached to it pass partly to the posterior part of the larger segment, and partly to the septal one. The latter cusp derives most of its chordæ from the ventricular septum directly, although the bases of some of the fibres are occasionally muscular.

In the last edition of *Quain's Anatomy*,[1] it is stated that "a fibrous band, sometimes muscular, is often found stretching across the cavity of the right ventricle from the base of the anterior papillary muscle to the septum," the representative of the moderator band found in the Ox and other Mammals.

I have most carefully gone into the literature of this point, and in no English or Continental work on anatomy have I found it satisfactorily discussed. In nearly all books it is mentioned in a casual manner, and the reader is left to assume that the presence of this band in the human heart is occasional, and its nature variable. The two English text-books which are most definite regarding it are Cunningham[2] and Wilson.[3] King, who in 1837 described its position and supposed function, and who gave it the name of "Moderator Band," speaks of it as generally present, and often modified. Rolleston[4] refers to it in a similar way. Fothergill[5] discusses its function, but leaves it to be assumed that the band is only occasionally present.

In the 100 hearts examined, I never once found this "moderator band" absent, although in some fifteen cases its septal attachment was so low down as to almost give it the appearance of an ordinary trabecula. In every case it was a muscular band.

Arising in common with the anterior papillary muscle near or at its base, it passes obliquely upwards and inwards, and becomes attached to about the middle of the septum, rather nearer its anterior than its posterior aspect. Its size varies

[1] *Quain's Anatomy*, 9th ed., vol. ii. p. 846.
[2] *Dissector's Manual*, part i. p. 170.
[3] *Anatomist's Vade-Mecum*, 1880, p. 648.
[4] Harveian Oration, 1873.
[5] Fothergill, *The Heart and its Diseases*, 1872.

much. I have found it 1½ inches in length, and almost as thick as the little finger, at other times attenuated and short. Again, its septal attachment may be simple or radiating. But while its septal end thus varies both as regards character and position, its connection with the anterior muscle is constant. A second smaller band sometimes exists, attached to the ventricular wall nearer the apex, and which either passes across to the septum independently, or more commonly after a short distance blends with the larger one.

The band thus described in the human heart assumes, as is well known, very large proportions in the heart of the Ox.

In other Mammals this moderator band almost invariably exists. I have not had the opportunity of examining the heart in the Ornithodelphia or Didelphia. Of the Monodelphian heart I have studied those of Edentata, Ungulata, Sirenia, Cetacea, Rodentia, Carnivora, and Primates. In all of these the moderator band is present, and in most of them has proportions similar to that of Man. I shall therefore only select from my list one or two instances that call for special comment.

In a fine specimen of the heart of a Leopard in the University Museum, the two papillary muscles are of equal size, and the moderator band about half as thick again as the anterior muscle itself (448).[1]

The only Cetacean heart examined was that of the Pilot Whale (*Globicephalus melas*), which, through the kindness of Professor Struthers of Aberdeen, I had the opportunity of studying. In it the position and size of the band quite correspond with those of the human variety. The heart of the Dugong shows perhaps the most marked band of the entire series, and differs from most of the others in that its papillary end is not only attached to the anterior muscle, but has also a large separate origin from the ventricular wall near the apex (452).

Among the Ungulates, the hearts of the Horse, Red Deer (446), and American Elk (447) are remarkable for the absence of columnæ carneæ from the ventricles. In the Horse, however, the band is present in the normal position, but as a stout fibrous cord.

[1] The numbers are those of the Catalogue of the Anatomical Museum of the University of Edinburgh.

In the Camel the band is large, and shows in a marked degree a radiation at its septal attachment (449).

A condition so universal in the Mammalia, and which, according to my investigation, is invariably present in Man,—it is somewhat surprising that its constant presence in the human heart should have been so little noticed, considering the thousands of hearts which are examined annually, not only in the dissecting-room, but also in the post-mortem theatre. This is, however, probably due to the fact that the usual method employed in opening the ventricle (especially among pathologists) is that of transfixion, when, of course, the band is cut through, and its presence unnoticed. Of later years, this method has almost entirely been replaced by that of flap incision. Even when the chamber is opened by a flap incision, the band is often severed, as in the collapsed condition of the ventricle it lies close to the anterior wall.

I have found that the best method of demonstrating it, is to open the ventricle by a triangular flap, made by cutting transversely near the auricle, and vertically near the free margin of the ventricle. Its true position is also well seen by cutting off the right auricle, and dilating the tricuspid orifice by a small incision, when the condition of parts can be viewed from above.

In young and fœtal hearts the band is well marked, although perhaps relatively somewhat smaller.

Under normal physiological conditions, it cannot be doubted that the right ventricle is liable at times to become surcharged with blood, and that to this slight over-distension the character of its wall specially lends itself. To oppose this, two forces seem to be at work. Firstly, the "safety-valve" action of the tricuspid valve, so fully described by Wilkinson King[1] in his paper on the Heart, published many years ago, a paper whose merits are insufficiently recognised at the present day. Secondly, the various small bands, fibrous and muscular, which cross the cavity in its lower half especially, and which must to some extent help to antagonise over-dilatation.

In addition to these, I believe that the anterior papillary muscle largely counteracts over-distension of the right ventricle. When the cavity has become filled with blood, and the valve-flaps

[1] *Guy's Hospital Reports*, 1837, vol. ii. p. 122.

floated into position of closure, then the ventricle contracting, this papillary muscle not only fixes the cusps, pulling them towards the interior of the chamber, but reacts on the wall. Its latter influence, in the great majority of cases, is not confined to a single point on the wall, but, owing to the trabecular radiation at the attachment of the muscle, affects a considerable area. This secondary action is aided by the moderator band, which not only elevates the base of the muscle, but pulls it towards the septum.

The (almost) constant presence of this band in the Mammalian heart presupposes that it has some rôle to play in the contraction of the right ventricle. It is doubtless merely one of the fleshy trabeculæ; but its size, fixed relations, and position mark it off from the others. It has been generally taught that it directly "moderates" over-distension. This view, however, appears to be an incorrect one, as from what has been said above, it will be readily understood that the band acts as a "moderator" indirectly, and that through the anterior papillary muscle.

It seems to me also probable that a well-formed moderator band will serve largely by its contraction to direct the blood stream towards the pulmonary orifice.

In many specimens of dilated right heart, in which only the initial stage of the lesion had been reached, I found that the dilatation existed only posterior to the muscle and its accessory band. In a more advanced stage the cavity was dilated almost equally.

ON THE NATURE OF LIGAMENTS. PART VI. By J. BLAND SUTTON, F.R.C.S., *Hunterian Professor, Royal College of Surgeons, England.*[1]

(*Continued from Vol. XXII., N.S. Vol. II. p. 553.*)

The Vocal Cords and the Hyo-epiglottideus Muscle.

FOR some years I have intended to look into the morphology of the vocal cords for the purpose of ascertaining their relation to ligaments in general; but difficulty in obtaining the requisite material has long prevented me carrying out this intention. Dissections of the human larynx had served to raise in my mind the suspicion that the true vocal cords are modified portions of the thyro-arytenoid muscles, but the nature of the false cords could not be divined from studying the human larynx alone. My investigations commenced by a comparison of the extraordinary larynx of a Cetacean with that of Man, and then interpreting the parts with the help of some intermediate forms. The inquiry has served to bring out some facts and conclusions of great interest.

Our standard text-book of anatomy (*Quain*) describes the false vocal cord thus:—

> The superior thyro-arytenoid ligaments consist of a few slight fibrous fasciculi, contained within the folds of mucous membrane forming the false vocal cords, and are fixed in front to the angle between the alæ of the thyroid cartilage, somewhat above its middle, and close to the attachment of the epiglottis; behind they are connected to the tubercles on the rough anterior surface of the arytenoid cartilages.

Critical dissections of these ligaments show that, instead of being attached exclusively to the thyroid cartilage, they become connected with the pedicle or base of the epiglottis; embedded in these ligaments we find the cuneiform cartilages (Wrisberg's), and on tracing them backwards the fibrous bands will be found to send, from their points of attachment to the arytenoids, accessory slips to the cornicula laryngis (Santorini's).

[1] Read before the Anatomical Society of Great Britain and Ireland, Nov. 1888.

Let us now examine the laryngeal cartilages in a Porpoise. Their relations to each other are most easily studied in a young or fœtal Porpoise.[1] On referring to fig. 2, we recognise the epiglottis (E), whilst the long cartilage (C) is, as Professor Howes pointed out, an enormously elongated cornicula laryngis. The epiglottis in the adult, as in the young, is azygous, whilst the cornicula are separate throughout life, but are united by means of dense fibrous tissue. The extremities of the epiglottis and

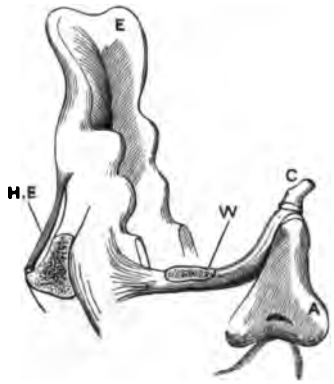


FIG. 1.—The human epiglottis, E; the false cord with Wrisberg's cartilage, W; the corniculum, C; arytenoid cartilage, A; the hyo-epiglottideus, HE (diagrammatic).

cornicula are swollen so as to enable the larynx to become "buttoned" into the soft palate, thus allowing it to be in the posterior narial orifice. The cornicula are separated from the cricoid by means of a cartilage representing the arytenoid (A) in fig. 2. This cartilage, as Howes has pointed out, can always be detected in the fœtus, but in the adult is invested by such dense fibrous tissue that it is difficult to detect it; indeed, many anatomists have regarded the combined cornicula and arytenoid as representing the arytenoid alone.[2] Howes' observations are perfectly accurate, and accord with the dissection of five por-

[1] The first specimen I dissected was a fœtus just born. An old female was following the mackerel shoals off Brighton, and, becoming entangled in the nets, received a blow on the head from a boat-hook. During the death-struggle the fœtus escaped from her vent, and was dexterously caught in a skip-net and at once forwarded to me.

[2] Professor Howes' paper in *Jour. of Anat. and Phys.*, vol. xiv. p. 467, "On Some Points in the Anatomy of the Porpoise," is well worthy careful perusal.

poise larynges which I have conducted. On examining the base of the corniculum a style-like process projects between the arytenoid and epiglottis to become connected by means of fibrous tissue with a piece of cartilage projecting from the base of the epiglottis. Some nodules of cartilage lie in this fibrous tissue.

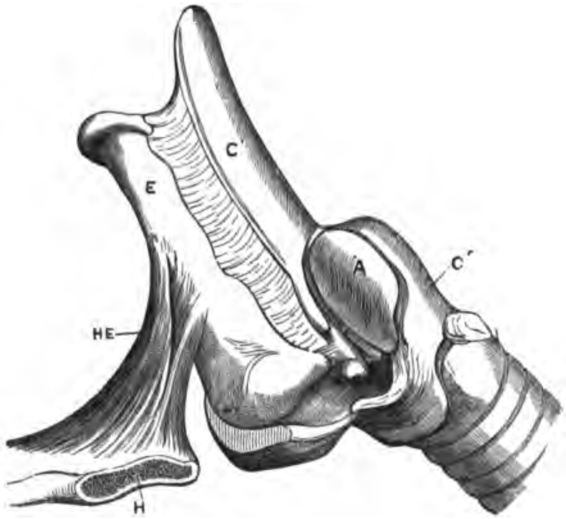


FIG. 2.—The larynx of a Porpoise. E, epiglottis; C, corniculum; A, arytenoid; C′, cricoid; HE, hyo-epiglottideus muscle; H, hyoid bone in section.

The Great Anteater (*Myrmecophaga jubata*) has a larynx which is very instructive in relation to my present purpose. The larynx of this Insectivore which I dissected has been in my stores some six years; it was selected on account of its presenting to a well-marked intra-narial epiglottis.

In *Myrmecophaga* we find the epiglottis well developed; passing from and directly continuous with its base is a rounded piece of cartilage, which passing backwards becomes directly continuous with a piece of cartilage overtopping the arytenoids. This rod of cartilage causes a projection of the laryngeal mucous membrane, and forms the false vocal cords. In this case it is clear that the cartilage stretching from the base of the epiglottis to the top of the arytenoid represents the superior

thyro-arytenoid ligament, with the cuneiform cartilage and corniculum laryngis of man.

In the Horse we find a thick piece of cartilage continuous with, and projecting from, the base of the epiglottis into the false vocal cords; whilst in a Bear (*Ursus himalayensis*) I found a condition of things very similar to that seen in *Myrmecophaga*.

Then, so far as Man is concerned, *the false vocal cords, with the cuneiform cartilages, are the degenerate representatives of the piece of cartilage by means of which the epiglottis and cornicula were originally united,* and with the cornicula laryngis must be regarded as vestigial structures.

FIG. 8.—EWC, the epiglottis in the Great Anteater, with the cartilage representing the false cord, Wrisberg's cartilage, and the corniculum; HE, the hyo-epiglottic muscle; T, the thyro-arytenoideus muscle.

Having disposed of the false we must now turn to the true cords. They are usually described as the inferior thyro-arytenoid ligaments, and are composed of closely-arranged elastic fibres, attached in front to the middle of the receding angle of the thyroid cartilage, and behind to the base of the arytenoid cartilages. On close dissection they will be found intimately connected with the thyro-arytenoid muscle; indeed, many fibres of this muscle are directly continuous with the cords. This relation of the cords and muscle suggests, as has already been mentioned, that the cords have been derived from the muscle, the more so as the true vocal cords are struc-

turally tendon. This view is confirmed by an examination of the larynx in *Myrmecophaga.* In this mammal the cords are broad bands, lacking the sharp definite edges seen in *Primates;* the thyro-arytenoid muscle too is round and compact in appearance; when this muscle is dissected away the true cords also disappear. An examination of the muscle teaches us that it is absolutely devoid of tendon, except that aspect of it which is immediately subjacent to the laryngeal mucous membrane; here the surface of the muscle presents a glistening tract of fine, thin, delicate tendons, constituting the true vocal cord.

In the Horse a similar disposition of muscle may be seen, and after dissecting away the thyro-arytenoideus and examining the vocal cords, we shall find them to contain tracts of muscular tissue.

Upon these facts I venture to regard the true vocal cords *as arising from the tendinous metamorphosis of those fibres of the thyro-arytenoideus muscle subjacent to the laryngeal mucous membrane.*

In order to make the hypothesis complete, it requires a case in which the vocal cords in Man have been found composed in part or wholly of muscular tissue; at present no such specimen is known to me, but possibly, now that attention is drawn to the matter, such a specimen may before long be forthcoming.

I feel convinced that such a condition will be seen, especially when we remember that the auriculo-ventricular valves of the heart are modified muscular tissue, and in at least one case a patch of striated muscle has been detected in the anterior flaps of the mitral valve of an adult.[1]

The Hyo-epiglottideus Muscle.

In the Horse, a muscle named hyo-epiglottideus may be found lying beneath the mucous membrane which constitutes the glosso-epiglottic fold. The fibres are somewhat pale, and it is embedded in the fatty tissue at the root of the tongue, immediately adjacent to the base of the epiglottis. The muscle is fusiform in shape, and arises from the lingual aspect of the epiglottis, and passes to an insertion in the hollow of the glosso-hyal; near its insertion the muscle sends off two lateral portions

[1] Dr John Ogle, *Trans. Path. Soc.*, vol. ix. p. 109.

to be attached to the cerato-hyal (lesser cornu of Man) on each side. Various unsatisfactory explanations have been advanced to its use, but in the Horse it is best regarded as vestigial.

In the Porpoise the hyo-epiglottideus arises from the dorsal aspect of the basi-hyal as two distinct muscles, but they soon fuse into a single mass of some size, and gain an insertion into the median ridge on the lingual aspect of the epiglottis by means of a distinct tendon. In some Cetaceans (*Globiocephalus*) it has been seen double.

In Man, a stout bend of fibrous tissue passes from the lingual aspect of the epiglottis, and is attached to the upper and anterior aspect of the basi-hyal; this, the hyo-epiglottic ligament, is the degenerate representative of the muscle of that name, as seen in the Whale[1] and Horse; it is well developed in *Myrmecophaga*, in *Ateles*, and very many mammals.

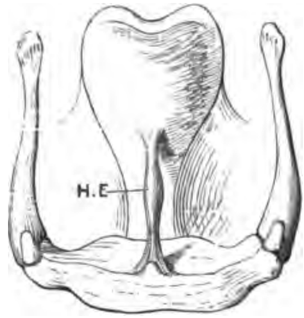


FIG. 4.—The hyoid bone and epiglottis of Man, showing the hyo-epiglottideus muscle, H.E. (From a dissection and drawing made by Mr Carwardine.) Semi-diagrammatic.

The homology has not been declared, simply because the band of tissue in question corresponds in attachment to the origin and insertion of the muscle it is supposed to represent, but because on two occasions I have seen it replaced by a distinct hyo-epiglottideus muscle[2] (fig. 4). Its point of insertion into the basi-hyal is of some interest. In the Horse a stout process

[1] Murie, *Trans. Zool. Soc.*, vol. viii., "On the Organisation of the Caaing Whale."

[2] The accomplished dissector of the Royal College of Surgeons, Mr W. Pearson, tells me that he has detected muscular fibres in the hyo-epiglottic ligament, and it is to Mr Pearson's skill I am indebted for the beautiful preparations illustrating my paper.

projects from the middle of the basi-hyal, and is known as the glosso-hyal; it is into this process that the hyo-epiglottideus is inserted, as well as into the basi-hyal. In Man the glosso-hyal is indicated by a small tubercle in the centre of the basi-hyal. There is in the Museum of the Royal College of Surgeons a hyoid bone in which this, the glosso-hyal, is indicated by a rounded process of bone one-sixteenth of an inch in length.

The conclusions arrived at in this study may be conveniently summarised thus:—

1. The true vocal cords, or the inferior thyro-arytenoid ligaments, arise from the tendinous metamorphosis of those fibres of the thyro-arytenoid muscle subjacent to the laryngeal mucous membrane.

2. The false vocal cords, or the superior thyro-arytenoid ligaments, represent, with the cuneiform cartilages, in a degenerate manner, an old communication between the epiglottis and the corniculum laryngis; the corniculum is in itself a vestigial structure in most mammals.

3. The hyo-epiglottidean ligament in the human subject is the fibrous representative of a well-formed muscle in many mammals.

Finally, in spite of great temptation, I have avoided all matters purely speculative, especially questions relating to the subject of the primary function of the larynx, for I believe the original function of the vocal cords is to protect the air passages, speech being a superadded function.

I had intended to deal with the thyroid cartilage and the thyro-hyoid ligaments with their cartilago-triticea, but this question, though well worthy of investigation, requires much more time than I can devote to it at present.

Note.—In the discussion which followed the reading of the paper, Professors Stewart and Thane regarded it as unlikely that muscular tissue should metamorphose into such highly elastic tissue as is found in the true vocal cord. This is paralleled in the case of the *tensor patagii* and other muscles in the wings of birds, some of which are occasionally entirely replaced by exceedingly elastic tendon, perhaps even more elastic than the vocal cords of man.

RABBIT WITH AN INTRA-NARIAL EPIGLOTTIS, WITH A SUGGESTION CONCERNING THE PHYLOGENY OF THE MAMMALIAN RESPIRATORY APPARATUS.[1] By G. B. HOWES, F.L.S., F.Z.S., *Assistant Professor of Zoology, Normal School of Science, and Royal School of Mines.*

DURING the past summer I had the good fortune to meet with the heads of two Rabbits in which the respiratory apparatus was modified, by way of complete enclosure of the epiglottis by the velum palati. Both individuals were young males in full health, and they measured respectively 17 inches and 19 inches in total length, from the tip of the snout to that of the tail. Seeing that, in details of departure from the normal type, I have been unable to detect the slightest difference between them, the description given below will apply to both—unless otherwise stated.

Intra-narial epiglottides (*i.e.*, epiglottides disposed permanently within the posterior narial passage) have been recorded in a number of mammals, as enumerated further on; but, so far as I can ascertain, no previous mention has been made of a like condition in the common Rabbit. I deem it advisable, therefore, to put the fact on record—partly in the interests of the elementary student in our native schools, but chiefly with a view to directing the attention of anatomists in general to a phenomenon which, as I endeavour to show in the sequel, is one of more general occurrence and deeper significance than has hitherto been supposed.

The tracheal tube of the Rabbit is of comparatively slight build. It usually runs, for the greater part of its course, side by side with, and to the right of, the œsophagus; on nearing the mouth it passes ventrally, to assume the relationships common to all normal mammals. The larynx itself is in no way remarkable for any special structural features, and its epiglottis

[1] Read before the Anatomical Society of Great Britain and Ireland, November 1888.

lies, in ordinary, on the floor of the mouth and but slightly uplifted. The velum palati is, as compared with that of other mammals, of full average length, and in the position of its posterior free border, there is considerable individual variation.

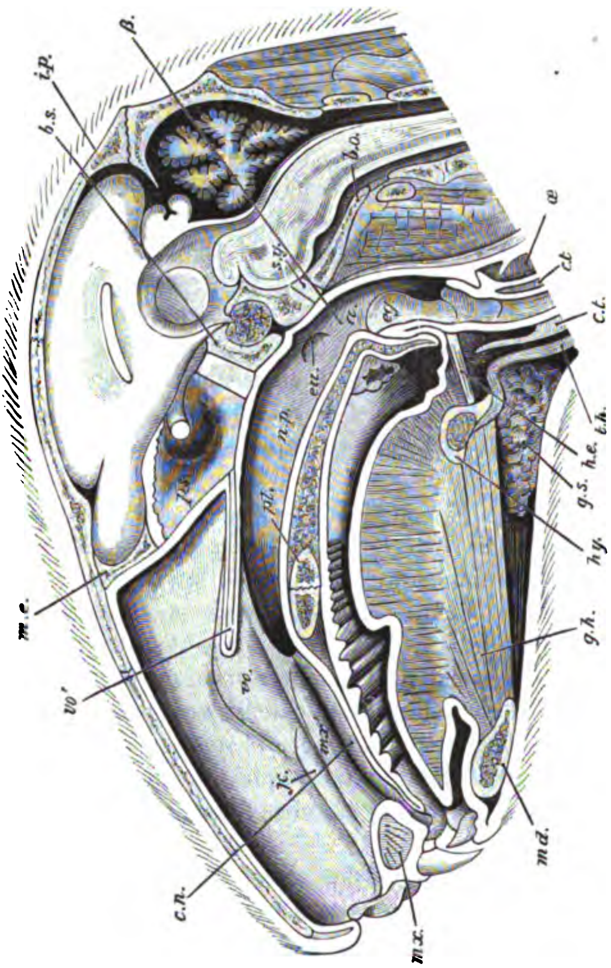


FIG. 1.—Rabbit with intra-narial epiglottis—General dissection of the head from the left side. × 1½. *b.o.*, basi-occipital; *b.s.*, basi-sphenoid; *c.n.*, naso-palatine canal; *c.t.*, thyroid cartilage; *eg.*, epiglottis; *eu.*, Eustachian orifice; *g.h.*, genio-hyoglossus muscles; *g.s.*, submaxillary gland; *h.e.*, hyo-epiglottidean muscle; *h.y.*, body of hyoid; *i.p.*, inter-parietal; *j.c.*, Jacobson's cartilage; *md.*, cut edge of mandible; *m.e.*, mosethmoid; *m.x.*, pre-maxilla, symphysial face of; *mx'.*, palatine process of pre-maxilla; *n.p.*, posterior narial passage; *œ.*, œsophagus, *p.l.*, hard palate; *p.s.*, pre-sphenoid, basi-palatine process of; *s.y.*, occipito-sphenoidal synchondrosis; *t.h.*, thyro-hyoid muscle; *vo.*, vomer; *vo'.*, cut edge of wing of vomer (bony floor of nasal capsule); *a. β.*, line marked, referred to in text (p. 264). The hyo-epiglottidean muscle is represented as seen in another specimen. It was represented in ligament in the one here figured.

I find, however, on examination of a large series of specimens, that this usually lies about on a level with a line drawn through the tentorium and occipito-sphenoidal synchondrosis—(*a. β.* of fig. 1 [*cf.* Parker's *Zootomy*, fig. 64, p. 334])—slightly posterior,

that is, to the free border of the epiglottis. The conditions were otherwise in the two individuals in question, for the epiglottis and side walls of the larynx were, in both, firmly embraced by the free end of the velum (see fig. 1).

Two suggestions at first presented themselves—(1) Had not the epiglottis merely become displaced, out of that position in which it is usually found on *post-mortem* examination, by a stertorous action induced under chloroform? (2) Supposing the epiglottis to be introduced into the posterior narial passage at every respiratory recurrence, as is not unlikely, might not its activity have been arrested at the moment of introduction? The first supposition was dispelled by the fact that in both cases the animals had died with the head fully extended, and in a position fatal to such displacement. The second one was found to be untenable, seeing that, even in the fully extended state, the embrace of the velum took place at an altogether lower level than would be the case were the epiglottis, as it exists in ordinary, merely inserted into the posterior narial passage. That the velum had grown back and enclosed the epiglottis was certain—firstly, by virtue of the point of termination of the former, at some distance behind the line referred to above (α. to β. of fig. 1); and, secondly, by the normal proportions of the epiglottis itself.

I have been unable to detect any structural detail of importance with respect to which these two larynges and their intrinsic muscles differ from the normal one, as described by Krause.[1] It is, however, worthy of remark that in the specimen figured the mucous membrane of the outer face of the epiglottis was slightly swollen above the point at which the embrace of the soft palate was firmest (*cf.* fig.), while the edge of the latter was, together with the adjacent pharyngeal mucous membrane, thickened at the same point, in excess of that which is normal, for purposes of special embrace. The larynx was firmly held within the posterior narial passage, and the parts were so disposed that food material must, during deglutition, have passed clear of the aditus, expiration and inspiration being alike possible only through the nose.

The above recorded facts at once suggest the condition of the

[1] "Die Anat. des Kaninchens," *Zweite Aufl.*, Leipzig, 1884.

parts so well known in the toothed Whales,[1] and that acquired in the young marsupial on reaching the pouch, and these would appear to be but further extensions along the same lines. Intranarial larynges of a more or less pronounced form either occur or have been described in the following orders of mammals, viz.:—*Cetacea* (*op. cit.*), *Ungulata*,[2] *Rodentia*,[3] *Proboscidea*,[4] *Insectivora*,[5] *Edentata*,[6] *Carnivora*,[7] *Marsupialia* (*vide supra*). A goodly category—and in the animals enumerated all grades of modification are represented, from the least modified term in the series (Canis), where the epiglottis is to be found, in individuals of the species, alone inserted into the posterior narial passage, to the most modified (Delphinidæ), where the whole larynx is attenuated and permanently buttoned into position, beyond possibility of withdrawal. Be the conditions what they may, the epiglottis is first and foremost in entering into the supposed new relationship.

In the case of the Cetaceans cited, the physiological significance of the facts is obvious. In certain other instances, how-

[1] First recorded (Porpoise) by Ray, *Phil. Trans.*, 1671, p. 2276; first adequately described by Hunter, *Ibid.*, 1787; and subsequently elaborated by Cuvier, Tyson, and cetologists to the present day.

[2] "PERISSODACTYLA," Equus, Chauveau, *Anat. comp. des animaux domestiques*, 2° édit.; "Et autre Solipeds," Milne-Edwards, *Leçons sur la Phys. et l'Anat. comparée*, t. vi. p. 271, 1860; "Rhinoceros," Flower, cited by Garrod, *Proc. Zool. Soc.*, 1873, p. 95; "Tapir," *cf.* Murie, this *Journal*, vol. vi., 1872, p. 138 and ref. "ARTIODACTYLA, RUMINANTIA," Camel and others; Savi, *Memoire scientifiche*, decade prima, 1824, p. 154; "Prongbuck," Murie, *Proc. Zool. Soc.*, 1870, p. 345. "NON-RUMINANTIA, Pigs and Hogs," *cf.* Owen, *Proc. Zool. Soc.*, 1851, p. 69; "Hippopotamus," Clarke, *Proc. Zool. Soc.*, 1872, p. 188.

[3] "Capybara," Morgan, *Trans. Linn. Soc. Lond.*, vol. xvi., 1833, p. 467; *cf.* Waterhouse, *Nat. Hist. of Mammalia*, vol. ii., 1848, p. 154. Lepus, *supra.*

[4] Cuvier, *Anat. Comp.*, 2° édit., t. iv. p. 600; *cf.* "Mojsisovics," *Archiv f. Naturgesch.*, 1879, vol. xlv. p. 56.

[5] "Hedgehog," Howes, this *Journal*, vol. xiv., 1880, p. 471 (*cf.* footnote on p. 269).

[6] "Dasyurus 9-cinctus," Owen, *Proc. Zool. Soc.*, 1831, p. 144—not confirmed by Murie in Tolypeutes conurus, *Trans. Linn. Soc. Lond.*, vol. xxx. p. 91, "Myrmecophaga" (?). The condition of the parts in this animal, as described and figured by Owen (*Trans. Zool. Soc.*, vol. iv., 1862), seems to me most intelligible on a supposition that the epiglottis was, in life, in all probability intranarial, and that it had been displaced after death. My friend Professor G. Stewart has kindly allowed me to examine both this original head and a smaller one in his charge. The two are agreed in the matter at stake.

[7] "Lycäon," Garrod, *Proc. Zool. Soc.*, 1878, p. 374; "Dog," Huxley, cited by Howes, this *Journal*, vol. xiv., 1880, p. 471.

ever, attempts have been made to associate the less specialised conditions with deglutition;[1] and it is well to inquire upon what grounds that deduction has been drawn. The old belief in the valvular action of the human epiglottis is well-nigh exploded. One of the latest investigators in this field writes of it:[2]—"This organ is generally described by physiologists as a cartilage placed as a valve at the entrance of the larynx to keep food, especially liquid food, out of the respiratory passages, the author ascribing more or less importance to this function, according to his judgment. The laryngoscope has revealed the fact that the action of the epiglottis is not limited to this valvular movement;" and he sums up his conclusions in the words—"The epiglottis is not essential to deglutition, even of liquids . . . . it is an important organ in the modification of the voice."[3] If this be admitted for the much laryngoscoped human subject, the deduction aforementioned must stand in abeyance. We know, from actual observation, little or nothing in support thereof, and it finds a resting-place among those phantasies born of a too exclusive contemplation on self.

Setting aside the deglutition difficulty, nothing is clearer than that the intra-narial epiglottis must conduce to a more perfect concerted action of the passages of intake, if indeed it shall have no more important physiological significance. The aforegoing list makes no pretence at being an exhaustive one, and it is tolerably certain that a more searching examination of the scattered literature would reveal additional records of the kind referred to. Perusal of the list shows, notwithstanding its completeness, that an intra-narial epiglottis has been observed *post-mortem* in representatives of at least eight of the thirteen great orders of mammals—the exceptions being the *Primates*,[4] *Cheiroptera* (?), *Hyracoidea*, *Sirenia*, and *Monotremata*. If the literature recorded be consulted in detail, it will be found that in the majority of cases the original observers were not in special search of the structural peculiarity in question; and there is evidence to show that (owing to no fault of the investigator's)

[1] *Cf.* Milne-Edwards, *Leçons sur la Phys. et l'Anat. comp.*, t. ii. pp. 271–73, 1857; and t. vi. pp. 268–71, 1860.

[2] Walton, *Jour. of Phys.*, vol. i., 1878–79, p. 313.

[3] *Loc. cit.*, p. 303.

[4] (?) *Cf.* Owen, *Comp. Anat.*, vol. iii.; "Mycetes," fig. 471.

it has probably been overlooked in some few marked cases.[1] There is no part of the mammalian body more liable to displacement in the process of ordinary dissection than the larynx; and it is in the highest degree probable (especially if, as analogy to the human subject would suggest, the epiglottis is in most instances introduced into the posterior narial passage during each respiratory cycle) that renewed examination of the parts, under special precautions and in the undisturbed state, will reveal a much more general enclosure of at least the epiglottis by the velum palati than might at first be imagined. I know of no method better suited to the requirements of the case than that of dissecting to one side of the middle line, as depicted in the fig.; a more longitudinal cleavage will not suffice; the head must be first rigidly fixed without stretching or unnatural displacement, the parts of the exposed side being then removed piecemeal until the desired level is reached.[2] The only alternative method is that of the frozen section.

It is impossible to contemplate the parts above dealt with without being struck with the constantly recurring tendency towards enclosure of the epiglottis by the velum palati in the majority of the mammalian orders. It becomes an interesting question, therefore, whether that may not have been the condition in the ancestral mammals (*Hypotheria* of Huxley),[3] and that it was for the purpose of thus completely restricting the main respiratory passage that the velum palati was first formed,[4] this presumed original condition having become modified or lost, under secondary adaptation of the epiglottis to phonation. The absence of the condition in quest in the Monotremes cannot, to my mind, be admitted as necessarily an argument against this deduction, they being the specalised survivors of their

[1] "Hystrix," Dobson, *cf.* footnote on p. 269; "Myrmecophaga," (?) Owen (*op. cit.*).

[2] The two Rabbits' heads above described were, as a matter of fact, the fortunate exceptions to forty dissected in this manner (by my students in a recent class), and that on the suspicion that something akin to what is here recorded might be encountered. I have since seen the same condition in two out of twenty individuals more recently dissected.

[3] *Proc. Zool. Soc.*, 1880, p. 658.

[4] I do not wish to imply that the Delphinoid condition was the primitive one (Albrecht alone could be capable of that, *Anat. Anzeiger*, vol. i., 1886, p. 338); on the contrary, it is the most specialised one.

stock. In *Ornithorhynchus*, admitted by general consent to be the least modified of the three living genera, the velum palati extends back to the base of the epiglottis. I am firmly of opinion that, under sufficiently careful observation, it will be found to enclose the same in this animal, if not in the *Echidna* also. I am strengthened in my belief generally, by the condition of the parts in the *Insectivora* and *Edentata* named, these animals being, in many important respects, on an admittedly lower structural platform than most living mammals, and approximating towards a type from which at least all the higher placentalia have arisen. In the Hedgehog individually, the complete embracing of the larynx by the posterior narial wall of the velum might, at first sight, appear to be in some way adaptive to the peculiar habits of the animal. There has gone on here, in all probability, a certain amount of such specialisation, but Dobson's[1] assertions that "the form of the larynx closely resembles that of *Gymnura*," and that the epiglottides of *Centetes*[2] and *Solenodon*[3] differ from those of Gymnura and Erinaceus in their "accuminate apex," at least suggest that that is not the whole explanation, and that a similar condition may yet be observed among other Insectivora.[4]

Appeal to the few known facts of development does not avail much. Between the periods of development of the velum palati and of full differentiation of the epiglottis there is a considerable interval,[5] and my friend Dr Bowles has shown me a series of preparations[6] which prove that, in the Pig, it is only during the first six months of extra-uterine life that the epiglottis comes to assume the intra-narial position. It must not be forgotten,

[1] *A Monograph on the Insectivora*, London, 1882–83, part i. p. 61.

[2] Page 85. [3] Page 95.

[4] Dr Dobson does not appear to have observed the condition recorded by me in any Insectivore. He, however, informs me, in correspondence, that he believes the same to be "common to all mammals when hybernating." Without wishing to discuss this ingenious suggestion, I would point out that I have found the intra-narial larynx in three of five Hedgehogs killed in the open during the non-hybernating period.

[5] Kölliker, "Entwicklungs d. Mensch. u. d. höheren Thiere," *Zweite Aufl.*, 1879, *cf.* pp. 467, 868.

[6] Made in connection with his work on Stertor in Animals. See *Trans. Med. Chirurg. Soc. Lond.*, vol. xlviii., 1870; and *Stertorous Breathing in Apoplexy*, Lond. British Medical Association, 1888.

however, that the epiglottis is, phylogenetically, a much older structure than the velum palati. We encounter it for the first time in the ascending series among the Amphibia,[1] and I think it not unlikely that the vicissitudes undergone in its development in the Mammalia (*cf.*, Man and Marsupial) may yet be explained under a "correlation of growth."

On turning to the purely physiological aspects of the question, there arise one or two further considerations. If the larynx of the Porpoise, with its related structures, be compared with those of the Elephant, or of the Rabbit figured above, it will be seen at a glance that diverse modifications are at work. In the first named animal the fully formed condition is arrived at by an excessive attenuation of the larynx; in the last named, by a backward extension of the velum palati. These opposite conditions might appear to be associated with similarly diverse modifications in the hyoid arch, that being complete and fully ossified in the first case, and incomplete laterally in the other two.[2] The coexistence in the Hedgehog, however, of a backwardly-extended velum, with a complete anterior cornu of the hyoid, would appear to be fatal to the suggestion.

In the Rabbit dissected there passed between the epiglottis and the body of the hyoid very obvious *hyo-epiglottidean muscles.* Krause asserts[3] that this muscle is represented in ligament in the form of a "langes, festes, fibröses Band;" and, further, under the heading "Varietät," he continues, quoting Hilgendorf, "Dors Lig. hyo-epiglotticum ist häufig muskulös: M. hyo-epiglotticum was für die Norm gehalten wird." In my specimen the muscle was paired; it was small, but definite, and passed on either side (*h.e.* of fig.) obliquely downwards and outwards from the base of the epiglottis to the body of the hyoid, in a manner suggestive of a median subdivision of its well-known homologue into two, similar to that recorded for Globiocephalus[4] and Balænoptera.[5]

Concerning the function of the hyo-epiglottidean muscle, little

[1] Howes, *Proc. Zool. Soc.*, 1887, p. 491.
[2] *Cf.* Krause, *loc. cit.*, p. 103; and Garrod, *Proc. Zool. Soc.*, 1875, p. 299.
[3] *Loc. cit.*, p. 210.
[4] Carte and Macalister, *Phil. Trans.*, vol. clviii., 1868, p. 237.
[5] Murie, *Trans. Zool. Soc.*, vol. viii., 1873, p. 264.

that is definite is known. Chauveau asserts[1]—"Ce muscle concourt à ramener l'épiglotte dans sa position normale après le passage du bol alimentaire. Mais il faut bien dire que l'épiglotte revient ainsi en avant surtout à cause de son élasticité propre et de celle des fascieux ligamenteux qui fixent cette pièce au cartilage thyroïde." If this hypothesis be tenable, it becomes difficult to account for the apparent absence of the muscle in Man, and for the fact that in many quadrupedal mammals the parts are so arranged that the posterior border of the velum appears to overlie the epiglottis, abutting against the ventral laryngeal wall. In such a case, did the epiglottis merely function, during deglutition, as a lid, the effect of its displacement would be simply that of forcing it back upon the velum palati. A flapping action in deglutition, as ordinarily understood, could manifestly only be possible in forms in which the velum stops short of the epiglottis; and, in view of the facts adduced by Walton in proof of the functional non-importance of the epiglottis in deglutition, I think it would be interesting to inquire how far we may not be dealing, in such cases, with the point of departure for the reduction of the epiglottis met with in certain forms (*e.g.*, Sirenia).

The hyo-epiglottidean muscle attains its greatest known development in Mammals having an intra-narial epiglottis (*e.g.*, Toothed Whales, Horse, Myrmecophaga (?). When viewed from the side in these, it gives the impression of being functional in maintaining the erection of the epiglottis rather than anything else.[2] If we picture that which would take place, under ordinary circumstances, in an intra-narial inspiration, it is clear that, under the elevation of the thoracic wall, by the scaleni and other muscles involved, a relaxation of the muscles of the sterno-thyroid series would ensue; this, reacting upon the parts of the larynx generally, would tend to induce a temporary folding over of the epiglottis. The latter, once initiated, would, under the suctorial action[3] of the parts, lead to disastrous results. Should

[1] *Loc. cit.*, 2nd edit., p. 481. (I have been unable to get access to a copy of Fürbringer's *Beitr. Zur Kenntniss der Kehlkopfmuskulatur*, Jena, 1875.)

[2] Murie writes (*Globiocephalus*, p. 264)—"Each is powerful, and must considerably influence the movements of the glottis, as taking their fixed point from the hyoid bone."

[3] Practical teachers will have experienced the need of a term indicative of this

this be actually the case, we should have a sufficient *raison d'être* for the great size of the muscle under the conditions specified, and ample grounds for associating it primarily with inspiration.

Further investigation is needed; the field is a wide one, and especially deserving the attention of the comparative physiologist. As the case stands, the facts point to "the uselessness of the epiglottis in deglutition,"[1] and, to my thinking, to a primary association in mammals between that organ and the velum palati, for purposes of respiration exclusively through the nostrils.

"suction pump" process. Without wishing to multiply names, I would suggest the introduction of the words *somatophysous* and *stomatophysous*—the former expressive of the processes at work (more especially that of the mode of inflation of the lung sac) in the higher amniota, the latter of the buccal "force-pump" process seen in the Ichthyopsida. (*Cf.* Huxley, *Anat. of Vertebrated Animals*, pp. 104-5.)

[1] Walton, *op. cit.*, p. 320.

THE ANGLE OF THE NECK WITH THE SHAFT OF THE FEMUR AT DIFFERENT PERIODS OF LIFE AND UNDER DIFFERENT CIRCUMSTANCES.[1] By Professor HUMPHRY, F.R.S.

I HAVE on several occasions expressed my doubt of the correctness of the still generally accepted statement, that the form of the upper part of the femur undergoes a change in advancing years—the angle of the neck with the shaft becoming lessened, and the level of the head of the bone being consequently lowered. I do not know of a similar change occurring in any other part of the skeleton. So far as I am able to judge, it is not usual for the form of the bones to alter after it has been fixed in the adult condition, even under variations of weight and muscular action, unless the force exerted upon them be brought to bear in some new and unusual direction; their curves and angles remaining the same from adolescence onwards under ordinary circumstances. The angle of the edentulous jaw, it is true, opens out, the gums of the upper and lower jaws being thereby approximated and rendered serviceable in mastication; but this results from the fact that the teeth and alveolary processes being removed, the pull of the powerful temporal, masseter, and internal pterygoid muscles is altered in direction, and the resistance to its tendency to elevate the angle of the jaw is lost in consequence of the removal of the parts just mentioned; and a physiological adaptation to the altered circumstances is thus brought about. Again, the vertebral column not unfrequently becomes bent in the aged, the dorsal curve being increased and encroaching upon or involving in itself the lumbar and the cervical curves, more particularly the former, and the bones may be correspondingly altered in form; but this results from the failure of the extensor muscles to maintain the trunk erect, which allows the weight to the head and thorax to bear unduly upon the fore part of the column. No similar contingencies await the head, neck, or other parts of the upper

[1] Read at the Meeting of the Anatomical Society, November 7, 1888.

region of the thigh-bone; and there seems no reason why it should undergo a change of form in the aged any more than the other bones of the lower limbs. If such a change did take place, it might manifest itself in a greater prominence of the trochanters and widening of the hips, with increased obliquity in the direction of the thigh-bones as they descend to the knees; and I am not aware that any such alteration has been observed in the figure of those who are advanced in years.

With the view of putting the matter to the test, I have taken the measurements of the angle of the neck with the shaft in thirty adult thigh-bones which happen to be in the Anatomical Museum of the University of Cambridge. The average length is 18½ and the average angle is 124°; but there is a good deal of variation. In some it is as low as 113°, 114°·5, 116°, and 119°; whereas in others it amounts to 130° and even 136°. On the whole, it is lowest when the bones are short, a considerable proportion of which may be assumed to be those of women. The average angle in those which are less than 18 inches in length (averaging 16½) is 122°·5. In those above 18 inches in length (averaging 19), a considerable proportion of which we may presume to be those of men, it is 125°. This difference is to be expected, because the elevation of the pelvis above the knee, together with the narrowness of the pelvis, opens up, as it were, the angle of the neck of the thigh-bone with the shaft. There are, however, greater deviations from this than might have been expected. One bone, for instance, measuring only 17 inches, has an angle of 130°; and another, measuring only 15½ inches, has an angle of 132°. On the other hand, two bones, measuring 18 inches, have angles of only 119°; and one, measuring 19½ inches, has an angle of only 114°·5. These discrepancies I do not pretend to account for. They may have had relation to variations in the distance between the knees in the different persons; but it is evident that they throw doubt upon the inferences drawn from the measurements of the angles of individual bones, whether senile or not. I may observe that in several of those in which the angle is low the shaft is somewhat flattened at its upper part, being expanded in the direction of the arc of the curve by the greater prominence and thickness than usual of that ridge, which normally descends from the lower part of

the neck upon the shaft, reminding of what is commonly observed in the curved bones in rickets, and serving the same purpose, namely, that of giving additional strength where it is needed by the presence of the curve.

I then took the measurements of the angles in fourteen thigh-bones from persons above the age of 70, in the Cambridge Museum, most of which I obtained myself, and of which I therefore know the ages. They are given in Table I. Considerable variety is here also observable. In one the angle is as low as 109°. It is an instance of extreme fatty degeneration, apparently from an old man; and there has been fracture, probably spontaneous, in the upper part of the shaft without any attempt at reunion, though the rounded edges and partially absorbed condition of the fragments indicate that the fracture is not very recent. I know nothing of the age or history of the case, the specimen having been sent me many years ago without any particulars; and it is evidently one of exceptional character. The others with low angles (116° and 113°) are from women, the one aged 96, who had been bedridden for two years, the other aged 76. In both these, more particularly in the latter, there is some of that flattening of the upper part of the shaft, and of that prominence of the line on its inner side, which I have remarked in adult bones with a low angle, and which may be taken as some indication that the low angle in these two instances is a natural conformation rather than a result of senile change. Against these three specimens with low angles must be set those in which the angles amounted to 128°, 131°, 137°, 128°, and 131°. In the remaining five the angles vary from 122°·5 to 124°·5. The average of the whole fourteen is 123°·7, which, though below the average of those in which the thigh-bone is more than 18 inches in length, is above that of those in which it is less than 18 inches; and seeing that nine of these fourteen specimens were taken from women, and that one, from a man, presents an abnormally low angle, the whole may be taken as offering a very fair mean, and certainly as offering no corroboration, of the view that this part of the skeleton undergoes any change of form in advancing years. Such change may take place in some exceptional cases, though it is not certain that even that is so; but it may be stated that, as a

rule, the angle of the neck of the thigh with the shaft is the same in the aged as in the adult.

Mr Griffiths, who was good enough to assist me in all these measurements, found the angle in thirty bones, in which he took it at Berlin, to be more open than in our Cambridge specimens, amounting on the average to nearly 128°. In the only specimen above the age of 70 which he found—a woman, æt. 74, in which the bone measured 18 inches—the angle was 130°.

In the Tables III. and IV. are measurements of thigh-bones in fœtuses and young persons, which, with one exception, are all from specimens in the Cambridge Museum; there are likewise considerable and unexpected variations in the angle of the neck with the shaft; but, all due allowance made for these up and down vibrations, it appears that, on the whole, a lowering of the angle takes place during fœtal life and in the periods leading from it to adolescence, the time that is when growth is completed. In the youngest fœtus taken (2½ months, where the bone measures 1 inch) the angle is 141°, and from this to birth the angle varies from 138° to 127°, making altogether an average of 132°. In those after birth the average is 127°.

It may be observed here that the growth and conformation of the various parts of the skeleton, including the neck of the thigh-bone, are in great measure brought about by forces, which we may call developmental, acting more or less in opposition to pressure—pressure resulting from weight and muscular action. Under ordinary circumstances those forces are sufficient to effect the purpose and give the proper length and shape to the several bones. It is not, however, always so. In rickets, as we know, the forces of growth and ossification at the epiphysial lines, as well as that which gives the requisite chemical composition to the shafts, are defective. Hence the bones fail to attain their proper length, and are liable not only to bend in the shafts, but also to yield and bulge at the circumference of the epiphysial lines, which are unduly thick and soft. It is not that the cartilage growth is in excess. On the contrary, that growth takes place more slowly than natural; but the ossification of the cartilage, which takes place chiefly on the shaft side of the epiphysial lines, is actually and relatively still slower, and is also irregular, and this is the cause of the epiphysial lines being

thick, soft, irregularly ossified, and bulging. These imperfections in structure and form are of course noted during the period of growth; but after growth has ceased and the epiphyses are ankylosed to the shafts, these bendings and bulgings do not occur, and the form does not alter except under diseased conditions, such as *osteomalacia*, or low inflammatory states, such as *osteitis deformans*, or, as I have before said, under some strain or pressure in a direction which the bones are not calculated to bear.

This relation between pressure and growth may serve, to some extent, to determine the angle of the neck of the thigh-bone with the shaft in the following manner:—The epiphysial line, which carries the cap-like head of the femur, and upon which the growth of the neck depends, is nearly horizontal, its direction being such as most to diminish the risk of injury; and accordingly displacement here has very rarely been observed,[1] though it is not improbable that damage sustained at the epiphysial line by weight suddenly thrown upon it may be an occasional source of hip-joint disease in young persons. This being the direction and position of the epiphysial line, when growth is most free at its proximal or *inner* part the head of the bone will be carried more *upwards*, and the angle of the neck with the shaft will be increased. When, on the other hand, the growth at the distal or *outer* part is most free, the head of the bone will be carried more *inwards*, and the angle of the neck with the shaft will be less. Now, when the pelvis and hips are narrow, as in early life, or in cases in which the thigh-bones are long, the weight falling in a considerable measure vertically upon the heads of the bones, or rather upon their outer parts, will give free scope to the growth at the inner parts of the epiphysial lines, and allow the development or persistence of a wide angle between the neck and the shaft. But when the pelvis widens, or in cases in which the thigh-bones are short, the weight falling more upon the inner parts of the epiphysial

[1] The only instance of such an accident established by autopsy that I have read is quoted by Hamilton, in his "Treatise on Fractures and Dislocations," from the *Bulletin de la Société Anat.*, 1867, p. 283. Patient, æt. 15, run over by a waggon; the limb shattered and everted, and patient, unable to move it, died in a few hours; complete separation of epiphysis, which was attached to the neck by a strip of periosteum.

lines may tend to repress the growth of the neck in this situation, and lessen the angle between the neck and the shaft. This may account for the lessening of the angle during the approach to adolescence when the pelvis is widening, and especially in women, in whom the pelvis widens most, and in whom also the thigh-bone is short. The widening of the pelvis, moreover, throws out the hips, and increases the obliquity of the thigh-bones, which is especially the case when the latter are short; and it thus, in an additional manner, determines the line of weight upon the inner parts of the epiphysial lines. Hence, as we find, when the bones are short the angle as a general rule is low, this being especially the case when the pelvis is also wide, as in women; whereas in tall men, the thighs being long and straight, and the pelvis not wide, the angle is usually open, and the heads of the thigh-bones are raised well above the level of the trochanters.

Another result of my observations, which corresponds with the remarks already made, has been to show that in cases in which, from any reason, the weight of the body is not transmitted by the neck of the thigh-bone, the angle of the neck with the shaft remains open, or, what is very remarkable, seems actually to open out.

Thus in the skeleton, in the Cambridge Museum, of a child, about five, with hydrocephalus, in which it is obvious that the delicate limbs could not have borne the heavy head, and that the erect posture could not therefore have been assumed, the angle of the neck of the thigh-bone with the shaft on each side is 148°, the length of the bone being 9¼ inches. In the Museum at Vienna I found a similar skeleton with similar width of the angles. In the skeleton of a person, æt. 25, in the College of Surgeons, with huge hydrocephalic head, and limbs so slender as scarcely to be compatible with the erect posture, the angle is 129°. In a hydrocephalic child, æt. 23 months, in the Museum of the Pathological Institute at Berlin, the angle is 145°, the length of the thigh-bones being 5 inches; in another, æt. 4 years, it is 143°, the length of the bones being 6 inches; in a third, æt. 2½, it is 143°, the length of the bones being 6 inches; in a fourth, in which the length of the bones is 6 inches, the angle is 143°; in a fifth, in which the length of the bones is 4

inches, the angle is 135°. The measurements in these five Berlin specimens were kindly taken for me recently by Mr Griffiths. The angle is also 143° in the thigh-bone, measuring 15½ inches, from a man, æt. 21, whose limb had been paralysed from infancy, and which I removed at the hip-joint on account of disease in that joint. In another adult thigh-bone, measuring 15½ inches, in the Cambridge Museum, which may be assumed, from its extreme thinness, to have belonged to a paralysed limb, the angle is 130°. In the thigh-bones of a bedridden idiot in the same museum, which measure 15 inches, the angle is 128°. In a thigh-bone in the Museum of the Middlesex Hospital, which is very thin, as if from paralysis, and which was fractured, the angle is 132°; and in the Vienna Museum the angles in the skeleton of a young idiot, with slender, feeble, sprawling limbs, are also very open. It is further to be noted that in none of these adult specimens does the length of the bone reach to 16 inches. In all, therefore, the growth of the bone has fallen short of the average standard, although the angle in all exceeds it.. In all the excessive width of the angle is associated with deficiency of growth and deficiency of pressure upon the heads of the bones. The deficiency of growth we may assume to be due to the want of muscular action and the associated want of blood-supply; but the connection between deficiency of pressure upon the head of the bone and the width—greater than normal even in the child —of the angle of the neck with the shaft is highly interesting.

An illustration of the same point—the association of wide angle with absence of pressure on the bone—may be observed in some cases in which amputation in the thigh has taken place in early life. Thus in the stump of a thigh-bone, which measures 5 inches, and which was taken from a lad who died two years after the amputation, the angle is 142°. In a second, from a man whose limb was removed when he was quite young, the angle in the stump, which measures 6 inches, is 127°, that in the opposite thigh-bone, which measures 18½ inches, being 122°. In a third, on the other hand, from a man in whom the amputation was also when he was young, the angle of the stump, which measures 7 inches, is the same (115°) with that in the opposite thigh-bone, which measures 17¾ inches. In each of the two last-mentioned cases the head of the thigh-bone in the

stump and also the os innominatum on that side are smaller than on the opposite side. In a fourth specimen, from a man, æt. 60, who underwent amputation in the thigh thirty-six years before his death, who had used a wooden leg, the angle of the neck with the shaft is the same, 120°, in each of the two thigh-bones.[1] In a stump in the Museum of St Thomas's Hospital, which is very short, reaching an inch only below the lesser trochanter, and also very small, indicating a lapse of many years since the amputation, though the head of the bone has a fair average size, the angle is 127°. In a short stump in the Museum of the University College, which does not show evidence of great length of time since the amputation, the angle is 135°.

The variations in the angle which we have observed in different persons, under ordinary circumstances, forbid our drawing much inference from these specimens; and the two in which amputation took place in early life, and in which we are able to compare the angles on the opposite sides, are rather conflicting. Still the specimens on the whole indicate that relief from the vertical pressure in a stump during the period of growth, tends to produce a wide angle of the neck of the thigh-bone with the shaft. It might have been thought that undue weight borne by the opposite limb would have led to some alteration in the angle on the opposite side, but the specimens do not indicate that this is the case.

The conclusions, therefore, at which I arrive are—

1. That the angle formed by the neck of the thigh-bone with the shaft varies considerably in different persons at any given period of life.

2. That it is smaller in short bones than in long bones; and that it is also most likely to be small when the pelvis is wide; the combination of these two conditions rendering it usually smaller in women than in men.

3. That the angle decreases during the period of growth; but that after growth has been completed it does not usually undergo any change, even if life be continued to extreme old age. Some change may take place in exceptional cases, but as a rule the angle remains the same from the adult period till death, at whatever age that may occur.

[1] These four specimens are in the Cambridge Museum.

4. That, if during growth the limb be relieved of the weight of the body, as in the bedridden state, in paralysis, or in a stump, the angle of the neck with the shaft usually retains the open form of early life, or even may become wider.

ANGLE OF NECK OF THIGH-BONE WITH SHAFT.

TABLE I.—*Senile above* 70.

No.	Sex.	Age.	Length of Bone.	Angle.
1.	F.	103	16½ inches	122°·5
2.	M.	88	...	128°
3.	M.	Aged	...	131°
4.	M.	76	...	137°
5.	F.	76	...	131°
6.	F.	71	...	122°·5
7.	M.	76	...	122°
8.	F.	96	...	116°
10.	F.	76	...	123°
11.	M.	Aged	Fatty degeneration	109°
12.	F.	70	...	124°
13.	F.	Edentations very old	18 inches	131°
14.	F.	86	15½ ,,	125°·5

TABLE II.—*In Atrophy.*

No.	Sex.	Age.		Length of Bone.	Angle.
1.	M.	21		15½ inches	143°
2.	,,	Adult		15½ ,,	130°
3.	,,	,,		15 ,,	120°
4.	,,	...		... ...	132°
5.	,,	5	(Hydrocephalic)	9¼ ,,	148°
6.	,,	25	,,	... ...	129°
7.	,,	23 months	,,	5 ,,	145°
8.	,,	4 years	,,	6 ,,	143°
9.	,,	2¼ ,,	,,	6 ,,	143°
10.	,,	...	,,	6 ,,	143°
11.	,,	...	,,	4 ,,	135°

ANGLE OF NECK OF THIGH-BONE WITH THE SHAFT.

TABLE III.—*Fœtuses.*

No.	Age.	Length of Bone.	Angle.
1.	2½ months	1 inch long	141°
2.	4½ ,,	1⅜ ,,	135°
3.	4½ ,,	1⅜ ,,	131°
4.	4 ,,	1⅝ ,,	131°
5.	4 ,,	1¼ ,,	138°
6.	5 ,,	2⅛ ,,	131°
7.	6½ ,,	2¼ ,,	127°
8.	7 ,,	2⅜ ,,	127°
9.	7 ,,	3 ,,	134°
10.	8 ,,	3 ,,	130°
11.	9 ,,	3¼ ,,	128°

Table IV.—*Young Persons.*

No.	Sex.	Age.	Length of Bone.	Angle.
1.	...	$3\frac{1}{2}$	7 inches	131°
2.	...	$3\frac{1}{8}$	...	130°
3.	...	6	$10\frac{1}{4}$,,	120°
4.	...	10	$9\frac{3}{4}$,,	120°
5.	...	15	$14\frac{1}{2}$,,	130°
6.	...	18	18 ,,	127°
7.	Female	19	$14\frac{3}{4}$,,	130°
8.	,,	20	$16\frac{3}{4}$,,	122°

THE POSITION OF THE MAMMALIAN LIMB; REGARDED IN THE LIGHT OF ITS INNERVATION AND DEVELOPMENT.[1] By A. MELVILLE PATERSON, M.D., *Professor of Anatomy in University College, Dundee.*

INTRODUCTION.

THE early stages in the development of the mammalian or avian limb show that it consists at first of an undifferentiated mass of formative tissue, derived from an outgrowth of portions of the intermediate cell mass, on the ventro-lateral aspect of the primitive segmented trunk of the embryo. The intermediate cell mass is at first segmented; but those portions of it from which the limbs are produced are (from the first appearance of the latter) fused together; so that, in its earliest condition, the limb itself, as such, presents no sign of segmentation. I have shown elsewhere,[2] that the bones and joints, and the whole of the muscular apparatus belonging to the limb proper, are a result of the differentiation of the mesoblast of which the limb-bud is composed. The skeletal elements are evidently distinct from, and superadded to, the skeleton of the trunk; nor is there, in my opinion, any convincing evidence to show that they are the descendants of gill-arches. The *muscles* of the limb, again, are originally in an entirely different plane from the trunk muscles; they grow at right angles to the trunk, whereas the axial muscles are arranged primitively in a longitudinal direction. Nor are they derived from the same source. The trunk-muscles are formed by a growth in a ventral direction, and a fusion together of the elements of the muscle-plates. The muscles of the limbs are perfectly distinct from these, as in the regions where the limbs are sprouting the muscle-plates do not, as elsewhere, grow round the trunk, but stop short at the root of the limbs. The *nerves*, however, which form the limb-plexuses,

[1] Read in the Section of Anatomy and Physiology at the meeting of the British Medical Association, Glasgow, August 1888.

[2] *Quart. Jour. of Micr. Sci.*, August 1887.

and are distributed to the limbs, we can regard as more trustworthy guides in forming comparisons, and establishing homologies on a sure foundation, than any of the other structures present in the limb, for two important reasons. In the first place, the nerves have reached the extremities and surfaces of the limb-bud, at a period when there is no sign whatever of the differentiation of the mesoblastic tissue into cartilage and muscle. In the second place, the nerves are the sole representatives of segmentation present in the limbs. They are the only segmental structures present. This fact was first pointed out by the late Professor Goodsir,[1] as far back as 1857. He first recognised the importance of the nerves of the limb-plexuses in indicating the segmental nature of the limbs; and enunciated the fundamental principle that "*the nervous elements of the limbs appear, as in other parts of the vertebrate animal, to indicate most distinctly the morphological constitution of the sclerous elements.*"

It is to the innervation of the limb then, rather than to its osseous or muscular characters, that we must look to obtain a correct idea of the primitive conditions or original type on which the foundations of the limb are laid, and with which we can compare the complex arrangements of the parts in the adult.

The Position of the Limbs.

An examination of the distribution of the nerves to the limbs, enables us to form a fairly accurate estimate of the position of the limbs in relation to the trunk. The nerves form our only evidence of the existence of segments; while the trunk retains its primitive segmental characters throughout, in the limbs there is no other evidence of original segmentation than that afforded by the nerves. Premising, then, that the nerves may be looked upon as in a sense representing segments, we may further infer that, when the *whole* of the inferior primary division of a nerve passes to the limb, then the limb contains as well a maximum portion of the formative material of the corresponding segment. Again, when only a part, large or small, of a nerve enters the limb-plexus, we may infer that the corre-

[1] Goodsir, *Edin. Phil. Jour.*, January 1857; reprinted in *Anatomical Memoirs*, edited by Prof. Turner, vol. ii. p. 201, 1868.

sponding segment is only partially implicated in the formation of the limb. For example, in the fore-limb the whole of the 7th cervical segment may be considered as giving a maximum amount of formative material to produce the limb, from the fact that the whole of the inferior primary division of the 8th cervical nerve is concerned in supplying the limb; on the other hand, a portion only of the 1st thoracic segment, and in exceptional cases, a still smaller portion of the 2nd thoracic segment, are engaged in its production.

Moreover, the whole of the inferior primary division of the nerve concerned is engaged in supplying the limb,[1] and not merely that portion which corresponds to the lateral branch, as Goodsir maintained.[2] The limb, thus, may be regarded as an outgrowth, opposite certain somites (the number of somites varying with the number of nerves supplying the limb), and from the ventral and lateral aspects of the primitive cylindrical trunk, corresponding to so much of these somites as agrees with the area of distribution of the whole of the inferior primary divisions of certain nerves (fig. 2). If Goodsir's hypothesis were entertained, the limb-bud must be regarded as springing from the lateral line of the body (fig. 3); and we should expect to find the ventral branches of the nerves (whose lateral branches would be distributed to the limbs) in the interval between the root of the limb and the middle line, on the ventral aspect of the body. This, however, we fail to do, as I have shown elsewhere. The distribution of a segmental nerve may be shown schematically, as in fig. 1. The superior primary division of the nerve supplies the dorsal third of the segment. The inferior primary division divides into somatic and splanchnic branches. The somatic branch divides again into ventral and lateral parts, which are distributed to the ventral and lateral thirds respectively. In fig. 2, the limb is represented as budding out from the lower two thirds of the segments with which it is connected, and from which it gets its nerve-supply; and not (as in fig. 3) from the lateral third alone, as would be the case if the limb nerves were homologous with lateral branches only. The dorsal and ventral branches of the somatic portions of the inferior

[1] Paterson, *Jour. of Anat. and Phys.*, vol. xxi. p. 611.
[2] *Loc. cit.*

primary divisions of the nerves, which are homologous with the lateral and ventral branches of the typical nerve, can be traced with ease, so far as the surfaces of the limbs are concerned, to

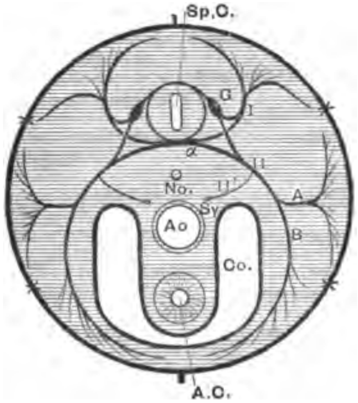


Fig. 1.

their respective dorsal and ventral surfaces, and in both extremities, both in man and other animals. It is in relation to the borders of the adult limb that difficulties arise, and it is a

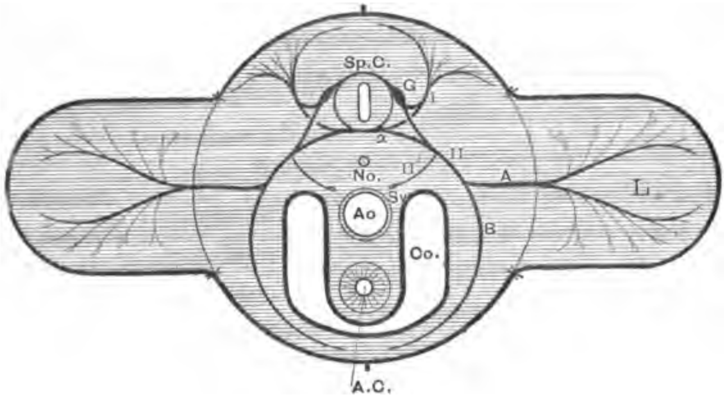


Fig. 2.

hard matter sometimes to define whether a given branch is dorsal or ventral, or partakes of the characters of both. The important and valuable researches of Dr W. P. Herringham,[1] and the laws which he has formulated regarding the disposition

[1] *Proc. Roy. Soc.*, No. 249, 1887.

of the nerves of the human arm, are here, however, of the greatest assistance, in making plain and distinct the picture of the distribution of the nerves to the limbs. His generalisations, made regarding the distribution of the nerves to the muscles and the skin of the human arm, are wide enough to serve for the fore and hind limbs of mammals generally. Connecting his conclusions with what has been stated above regarding the segmental value of the nerves of the limb-plexuses, we see that the nerves retain their position, and supply in the adult those parts of the limb which correspond to the segments represented by the nerves. While the limb grows further and further outwards from the trunk, the nerves, fully developed at an early

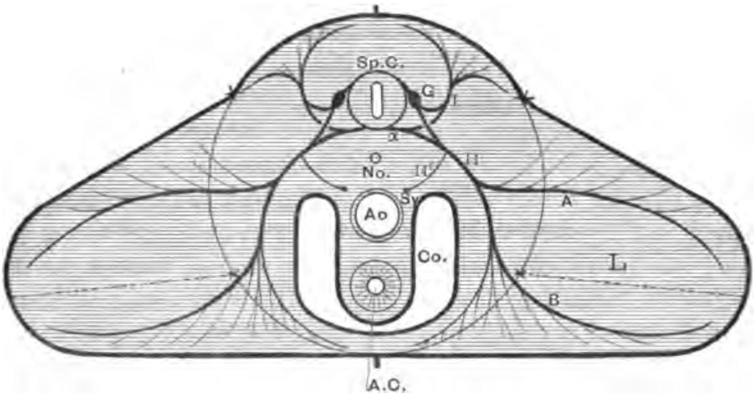


Fig. 3.

date, retain a primitive position; especially when considered with regard the pre-axial and post-axial borders, and to points placed proximally and distally in the surfaces and borders of the limb. The most pre-axial nerve in the plexus, for example, supplies the most proximal portion of the pre-axial border of the limb; the nerve behind it supplies a more distal portion of the same border; the post-axial nerves are distributed to the post-axial border, while the intermediate nerves supply the surfaces (between the borders) of the limbs.

A. The Position of the Fore-Limb.

While presenting variations in the *number* of nerves which supply it, and therefore of the segments of which it is formed,

the position of the fore-limbs in mammals is fairly constant, only presenting a few exceptions, and those nearly all alike. As a rule, the first thoracic nerve is the last to enter the brachial plexus. Out of twenty-five cases of the dissection of the plexus in different animals, many of them often repeated, this is the case in nineteen examples. In some of these it is possible, of course, that an intra-thoracic connection between the second and first thoracic nerves had been overlooked: in the ten cases dissected by myself, however, I can be certain of its non-existence, as in each the whole spinal system was dissected fully. In six animals (Man, Horse,[1] Sheep,[2] Ox,[2] Pig,[2] and Dolphin[3]) the second thoracic nerve completes the plexus posteriorly. Man is included in these exceptional cases, as Cunningham[4] has shown that in twenty-seven out of thirty-seven cases the second thoracic nerve joins the first within the thorax. Herringham[5] states also "that the ninth [spinal nerve] receives at its original a small branch from the tenth, *in the majority of cases.*" We have thus a fixed point for the origin of the proximal end, at least of the post-axial border of the limb, in the first or (in exceptional cases) in the second thoracic segment. The limb-segments may vary in number; the limb may be built up from more or fewer segments, extending forwards towards the head for a greater or less distance; but it is generally placed so that its post-axial border has an attachment to the trunk opposite the first or second thoracic segment. In the Camel, for instance, the nerves concerned in supplying the limb are the 6th, 7th, and 8th cervical, and the 1st thoracic. In Man the limb extends further, both forwards (to the 8th) and backwards (to the 10th segment).

The fore-limb, as a rule, then is derived in mammals from the posterior cervical, and part of the first thoracic, or rib-bearing segments. From the fact of the post-axial part of the limb at its proximal end being innervated by the greater part of the first thoracic nerve, we infer—(1) that that segment is partially

[1] Percivall, *Anatomy of the Horse.*
[2] Chauveau, *Comp. Anat. of Domesticated Animals.*
[3] D. J. Cunningham, *Jour. of Anat. and Phys.*, vol. xi. p. 209.
[4] D. J. Cunningham, *Jour. of Anat. and Phys.*, vol. xi. p. 539.
[5] *Loc. cit.*

represented in the construction of the limb; (2) that in most cases that is the last segment from which the limb is built up; (3) that the material derived from the limb-forming somites to produce it, is something which in the ordinary limbless somites of the body has either been lost, or has never been developed; because here we find a complete osseous and muscular segment; and yet at the same time engaged in the formation of the limb. From the exceptional cases, such as Man, we infer that these cases show a tendency for the post-axial border of the limb to spread in a caudal direction, so as to develop partially from an additional thoracic segment.

This inference is strengthened by an exception tending in the opposite direction. In the Manatee, as an example of an animal presenting an abnormal number of cervical vertebræ, the brachial plexus is formed by the last cervical nerves alone, and not at all by the first thoracic. The discussion which has been raised on the question of omission or interpolation of vertebræ appears to be a fruitless one. The evidence adduced by Murie,[1] and supported by Chapman,[2] for asserting that the third cervical nerve in the Manatee represents both the third and fourth, and that the third vertebra has therefore dropped out, is not strong, and has been confuted by Ray Lankester.[3] It seems, however, more probable that the absence or addition of a vertebra is to be explained, not by a hypothetical vanishing or interpolation, but by an increased or diminished development of correlated parts of the skeleton, and by variations in the position of the limbs with regard to the vertebral column. In the case of the Manatee two explanations are possible, without any need for supposing that a vertebra has dropt out in the neck. Either the limb occupies a primitive, archaic position, or it has been moved forwards towards the head, so as to allow, by its shifting, the development of the rib-elements of the eighth cervical vertebra to proceed to such a marked extent as to make it thoracic.

While, therefore, in mammals, as we shall see especially in relation to the hind-limbs, the tendency is for the limb to shift

[1] *Trans. Zool. Soc.*, vol. xi., Aug. 1880, p. 36.

[2] "Observations on the Structure of the Manatee," *Proceedings of the Acad. Nat. Sci. Philadelphia*, 1875, quoted by Murie.

[3] Garrod, "Notes on the Manatee recently living in the Society's Gardens," *Trans. Zool. Soc.*, vol. x. p. 137; Collected Works, p. 303.

backwards, in a case like this the movement may be a forward one instead.

Birds.—The last number of Bronn's *Thier-reichs* has recently appeared, containing the very valuable researches of Fürbringer and Gadow[1] regarding the constitution of the limb-plexuses of birds. Owing to the kindness of Dr Gadow, I was able to read their work at an early date, and so embody the conclusions contained therein in the present paper. In birds the brachial plexus is formed of 3–6 nerves, of which the pre-axial and post-axial are partially, the intermediate nerves wholly, distributed to the limb. Three nerves form the plexus in *Bucorvus abysinnicus;* six in *Charadrius* and *Columba;* the average being four or five. There are three varieties in the position of the plexus. Out of seventy-six cases, in forty-nine (*i.e.*, 64·5 per cent.) the plexus is formed by the last cervical nerves. In seventeen cases (*i.e.*, 22·4 per cent.) it is formed by the posterior cervical nerves alone, omitting the last. In ten cases (*i.e.*, 13·1 per cent.) it is formed by the last cervical nerves, with the first thoracic as well. The spinal nerves counted in series from the first vary extremely in number, according to the length or shortness of the neck. *Cypelus apus* (with 10th to 14th nerves) and *Cygnus atrus* (with 22nd to 26th nerves) present the extremes. Individual variations, and variations affecting the two sides, are also frequent in the construction of the plexus. These variations Gadow considers important, as they often occur along with a varying condition of the last cervical rib, or with unequal development of the cervico-dorsal transitional ribs. Fürbringer states that there is a certain limited correlation between the development of the brachial plexus and the neighbouring ribs. When the plexus is developed more anteriorly, presternal ribs are well formed. There are cases, on the other hand, when the plexus is placed further back, which show a considerable reduction in the posterior movable cervical ribs. Fürbringer explains these facts as indicating a shifting of the limb and brachial plexus towards the tail, in some cases towards the head.

These researches in birds point to the conclusions I have

[1] Bronn's *Klassen und Ordnungen des Thier-reichs*, sechster Bd., iv Abtheil. 18, 19, 20, Lief. 1888.

hinted at already, and which is still further borne out in the case of the hind-limb, that the position of the limb is not a fixed one, that it may move forwards or backwards, and that in consequence other correlated changes are brought about affecting the conformation of other parts of the body.

B. The Position of the Hind-Limb.

In its development the hind-limb follows a course similar to that of the fore-limb. Pursuing, therefore, the same line of argument as in the previous case, we may consider the nerves forming the limb-plexus as the only representative of segmentation, and the other structures of which the limb is composed as originally entirely unconnected with the vertebral somites. We thus find that the hind-limb is derived from a variable number of segments, but that the segments concerned are those ending posteriorly at a fixed and definite point, represented in the adult mammal by one of four segments—the last lumbar, the first, second, or third sacral vertebra.

In an examination of the hind limb-plexus, for the purpose at present in view, all those nerves may be left out of account which are not concerned in the supply of the limb proper. The nerves to be omitted are—in the terms of human anatomy—ilio-hypogastric, ilio-inguinal, and external cutaneous at the anterior end; and the nerves behind the *N. bigeminus* of Ihering at the posterior end. This is the nerve which assists in forming both sacral and pudendal portions of the sacral plexus; and it is therefore a good guide to the posterior end of the great sciatic nerve, as it forms in most cases the last root of that nerve and the first root of the pudendal plexus. The pudendal plexus comprises the small sciatic and pudic, and occupies a position posterior to or just about the level of the point of attachment of the post-axial border of the limb. They belong essentially to the perineum, and not to the limb.

The position of the small sciatic nerve in man is extraordinary. In no other mammal that I have had an opportunity of dissecting have I found it supplying much more of the limb than the fold of the flank. In the human subject the nerve seems to have been drawn down the limb, and so to have obtained an enlarged area of distribution in the process of straightening of

the knee and the assumption of the erect attitude. I would consider the nerve (so far as the primitive limb is concerned) as being distributed along its post-axial border; and from further observations, which need not be detailed here, would regard it as containing the elements (in man at least) of both dorsal and ventral branches of its component nerves, and not of dorsal branches alone, as stated in a former paper.[1] The gluteal branches are dorsal, the pudendal branches ventral, while the fine branches distributed down the thigh represent those destined originally for the primitive post-axial border of the limb.

The last spinal nerve, then, which must be taken into account as assisting in the formation of the nerves distributed to the hind-limb proper, is the *N. bigeminus*—that is, the last root of the popliteal (or great sciatic) nerves, and the first root of the pudendal plexus.

Out of nineteen animals, in nine cases the *N. bigeminus* was formed by the second sacral nerve; in other words, that nerve was the last to assist in the formation of the sacral plexus. The animals were:—Chimpanzee,[2] Fox,[3] Camel,[3] Brindled Gnu,[4] Rabbit,[4] Cuscus,[5] * Ox,[6] Pig,[6] and Horse.[7] In four animals—Capuchin Monkey,[4] Cat,[4] Porcupine,[4] and Guinea Pig[4]—the first sacral nerve was the most post-axial root of the great sciatic (or in other words, the *N. bigeminus*). In four animals—Entellus Monkey,[4] Koala,[4] Rat,[4] and Thylacine[5]—the plexus was limited posteriorly by the last lumbar nerve. In two cases—Man[8] and the Ass[3]—as many as three sacral nerves were implicated, the third being the last.

The series of cases quoted is far too small; but from the data

[1] *Jour. of Anat. and Phys.*, vol. xxi. p. 623.

[2] Champneys, *Jour. of Anat. and Phys.*, vol. vi. p. 211.

[3] Swan, *Comp. Anat. Nerv. Syst.*

[4] Paterson, *On Spinal Nerv. Syst. of Mammalia*, Graduation Thesis, Univ. Edin., 1886.

[5] Cunningham, D. J., *Jour. of Anat. and Phys.*, vol. xv. p. 265.

* There is a doubt here as to the exact limit posteriorly of the great sciatic nerve, as the small sciatic is described as arising from the great sciatic, and the spinal origin of the pudic is not given.

[6] Chauveau, *Comp. Anat. Domesticated Animals.*

[7] Percivall, *Anatomy of the Horse.*

[8] Paterson, *Jour. of Anat. and Phys.*, vol. xxi. p. 407.

at hand it is seen that the position of the mammalian hind-limb varies considerably in different cases, when examined in relation to the vertebral segments with which it is immediately connected. Its position is not so definite as in the case of the fore-limb. It varies less, however, in relation to the segments—lumbar and sacral—immediately adjacent, than it does in relation to the whole series of spinal segments, counted from the atlas backwards. I have shown elsewhere[1] that the 25th spinal nerve is the only one present invariably in the animals mentioned, and that the anterior end of the plexus may be placed anywhere between the 21st and 25th spinal nerves inclusive; its posterior end between the 25th and 29th spinal nerves.

The hind-limb is formed of elements derived from a variable number of somites, ending posteriorly with one of four. In the majority of cases, the first two "sacral" segments are the last involved. In fewer cases the limb is limited posteriorly by the first "sacral" or last lumbar segment; in still fewer cases as many as three "sacral" segments are involved.

In a majority of cases we find that the number of "true sacral" vertebræ corresponds with the number of sacral nerves which serve to complete post-axially the great sciatic nerve. In man there are three such vertebræ and three such nerves related to the limb. If this arrangement were constant, it would be an easy explanation of an otherwise difficult problem, and would effectually settle the question of sacral homologies, so far at least as mammals are concerned. The matter, however, is not so simple. The class Rodentia, for example, possesses but one "true sacral" vertebra, but it is not by any means an uniform arrangement to find the first sacral nerve limiting the plexus posteriorly; for while it is so in the rabbit and guinea pig, in the rat and porcupine the last lumbar nerve is the last to enter the plexus. Marsupials, again, possess only one "true sacral" vertebra, but in none of the examples mentioned above is the corresponding nerve the last in the plexus. In Thylacine and Koala the last lumbar is the last involved; in Cuscus the second (?) sacral nerve is the last to join the great sciatic.

[1] *Jour. of Anat. and Phys.*, vol. xxi. p. 620

In most cases, I apprehend, the true "sacral" vertebræ in mammals do represent the last segments with which the limb is connected; and this connection is maintained in the adult. In other words, *the post-axial border of the limb is in direct relation to the hindmost of the segments from which it is derived.*

In those cases, however, in which the nervous order differs from the osseous order, as a general rule, the bone or bones with which the pelvic girdle is articulated are *behind* the most post-axial nerve of the sacral plexus. For example, in such cases as the Porcupine, *Semnopithecus entellus*, or Thylacine, the last lumbar nerve completes the plexus posteriorly; hence it must be inferred that, in the process of development, after the limb-bud is formed, and the nerves have entered it, the limb *has shifted backwards*—has either been pushed backwards by the growth of the abdominal parietes or the development of the contained viscera, or has been drawn backwards so as to obtain a fixed point more suitable for purposes of progression. In consequence, while at an early period (as is actually the case and remains so in the adult in most cases) the hind-limb lies opposite to the segments from which it and its nerves are derived, at a later stage it gets fixed to segments placed farther back, and its nerves take a course obliquely backwards to enter it.

In those cases which (like Cuscus, the Ass, and Man) present the sacral plexus as completed posteriorly by nerves lying behind the true sacral vertebræ, or, in other words, in which the sacral vertebræ are increased by additional bones derived from the series in front, the inference is, that *the hind-limb has shifted forwards* towards the head, so as to cause assimilation of the hinder lumbar vertebræ into sacral, the nerves of the limb-plexus indicating the original primitive position of the limb. In man, therefore, we may regard the first sacral as an assimilated lumbar vertebra.

Rosenberg[1] has advanced the theory that, phylogenetically, a process of shortening of the vertebral column is going on in the human subject. Into this theory and the grounds on which it

[1] "Ueber die Entwicklung der Wirbelsaüle und das centrale Carpi des Menschen," *Morpholog. Jahrb.*, 1876, Bd. i. s. 83.

is formed we need not enter. He shows that, in the course of development, the innominate bone becomes adherent to the 26th, 25th, and 24th vertebra in succession. By this he explains the presence of an increased or diminished number of thoracico-lumbar vertebræ. The form of vertebral column with twenty-five movable vertebræ he regards as "ancestral;" the "future" form is the one with twenty-three movable vertebræ. In this way a process of headward shifting of the pelvic girdle is made out. Data with regard to nerve relations would help to confirm the theory. It would be interesting to know if, in cases presenting an additional thoracic or lumbar vertebra, the *N. bigeminus* were the 2nd instead of the 3rd sacral; or, in cases of absence of a thoracic or lumbar vertebra, if the 4th sacral nerve limited the plexus posteriorly.

Welcker[1] figures and discusses the condition of the lumbar and sacral regions of the vertebral column of six examples of *Choloepus didactylus*, none of which agree in the point of articulation of the innominate bone and vertebral column, and therefore in the position of the hind-limbs. The first sacral vertebra varies between the 32nd and 37th spinal segments. We are unable to say which may be regarded as the most primitive form in these examples, as no account is to be had of the nerve-relatives, the skeletons being drawn from different museums; but, without further inquiry, we have here clear evidence of a shifting of the sacro-iliac articulation either forwards or backwards.

Reptiles and Birds.—Avoiding, as far as possible, any discussion of sacral homologies, it is noteworthy, however, that in Reptiles and Birds variations are found in the relations of the nerves and the position of the limb corresponding to what has been described in the case of mammals.

In Reptiles,[2] in most cases, the limb is articulated to the vertebral column opposite to the segments in relation to which it is developed, so that the two true sacral vertebræ belong to segments which bear part in the formation of the limb. In a

[1] "Die neue Anatom. Anstalt zu Halle," *Arch. f. Anat. und Phys.*, p. 174, 1881.

[2] Mivart and Clarke, "On the Sacral Plexus and Sacral Vertebræ of Lizards and other Vertebrata," *Trans. Linn. Soc.*, ser. 2; *Zool.*, vol. i. p. 513; Gegenbaur, *Jenaische Zeitschrift*, Bd. vi. Heft. 2, 1871, p. 157; Hoffmann, *Niederländisches Arch. f. Zoologie*, Bd. iii. Heft. 2, 1876, p. 143.

minority of cases the "inter-sacral" nerve of Mivart and Clarke forms the bigeminus, and the limb has slipped backwards to be attached to a segment of the axial skeleton behind those with which it is developmentally connected. In such cases the 2nd "sacral" vertebra is not really representative of a segment related to the development of the limb.

In Birds we have also indubitable indications of a tendency towards a shifting of the hind-limb in a caudal direction, similar to what we have seen in the case of the avian fore-limb, and similar to what occurs, as a rule, in reptiles and mammals. Gadow[1] has collected a mass of evidence regarding the correlation between the position of the sacrum and the position of the sacral plexus in birds. He has examined over ninety examples, and shows that there are great variations in the condition of the acetabular vertebræ,[2] and that the position of the *N. bigeminus* in regard to them is by no means constant. He finds that assimilation of the acetabular group is constantly seen in the groups of vertebræ both before and behind, and that individual variations are present, as well as variations on the two sides.

SCOLIOSIS.—The view of the unstable position of the limb which is now advanced is supported by observations made by several authors on a form of congenital scoliosis, met with both in man and animals.

In *Man* it is doubtless rare to find any considerable degree of lateral curvature of the spine as a consequence of inequality on the two sides in the mode of the articulation of the innominate bones and sacrum. It does occur sometimes, however, as Welcker[3] has shown. There are numerous instances, however, in which the first sacral vertebra articulates with the innominate bone on one side only; presenting on the other side characters which approximate it to the lumbar series. In such cases a compensatory lateral curvature must result, in consequence of, and along with, the obliquity of the pelvis. In the instances in which there are only four sacral vertebræ, this condition points to a shifting caudalwards of the pelvic girdle, or at least an absence of the usual tendency to

[1] Gadow, *loc. cit.*, p. 409.
[2] Gegenbaur, *loc. cit.*
[3] *Archiv f. Anat. und Phys.*, 1881.

move headwards. When the sacrum possesses six vertebræ, and the first only articulates on one side with the innominate bone, we may infer (though our position would be stronger if we knew the exact condition of the sacral plexus) that there has been a shifting forwards of the limb-girdle, and a consequent assimilation of the last lumbar into a sacral vertebra.

In *Birds* Gadow[1] states that similar irregularities are frequently met with; the vertebræ which articulate with the ilium oftentimes presenting variations.

In *Reptiles*, also, such cases are not uncommon. Hyrtl[2] describes examples of scoliosis in *Ctenoden nigropunctatus*, *Oplurus torquatus*, *Lophura amboniensis*, *Grammatophora barbata*, *Chrysolamprus ocellatus*, *Bipes Pallasii*, *Menopoma alleghanense*, *Testudo græca*, *Chersina angulata*, *Clemmys cumberlandensis*, and *Pyxis arachnoides*. He also quotes instances in *Triton cristatus*,[3] and *Cryptobranchus japonicus*.[4] In all these cases the ilium articulates more or less normally with the vertebral column on one side, while on the other side it articulates with vertebræ placed farther back. He considers these cases as examples of assimilation of sacral into lumbar, and of caudal into sacral vertebræ. We may go even further and explain this assimilation as the consequence of the shifting backwards of the hind-limb in relation to the axial skeleton.

CONCLUSIONS.

The conclusions derived from the foregoing statements may be formulated as follows:—

1. The segmental spinal nerves which enter and supply the limbs afford the most trustworthy evidence regarding its original position.

2. The limbs may be regarded as outgrowths from the ventral and lateral aspects of certain somites, and from so much

[1] *Loc. cit.*, p. 407.

[2] Hyrtl, "Über Wirbelassimilation bei Amphibien," *Sitzungsb. d. k. Akad. d. W. Math. Naturw.*, cl. xlix. Bd. 1, 1864.

[3] A. S. Schultze, *Meckel's Arch. f. Phys.*, 4 Bd. p. 379, 1818.

[4] Schmidt, Goddart, u. Van der Hoeven, *Natuurk. verhand. v. d. Holl. Mattschapp i j d. Wetenschappente*, Haarlem, 1862.

of these as agrees with the distribution of the inferior primary divisions of the corresponding nerves.

3. From the evidence afforded by the nerves, the position of the mammalian limb is not constant in relation to the longitudinal axis of the body.

4. The position of the fore-limb varies only slightly, but it shows a tendency to shift towards the hinder end of the body. [This agrees with Fürbringer's conclusions in regard to birds.]

5. In mammals, with an abnormal number of cervical vertebræ, the irregularity is due, not to the interpolation or omission of vertebræ, but to a shifting of the limb, and a correlated difference in the development of associated parts.

6. The position of the hind-limb is less constant. While it may retain its embryonic position, in most cases it displays a tendency to move backwards. [This agrees with Gadow's conclusion in regard to birds.]

7. The "sacral" vertebræ, in consequence of this shifting of the limb-girdle, may not be strictly homologous with the corresponding bones in another individual or species. They simply serve a similar purpose in supporting the limb-girdle.

8. In certain exceptional cases, as in man, there is a tendency in the hind-limb for a shifting forwards of the limb-girdle in relation to the axial skeleton, along with a concomitant shortening of the vertebral column.

EXPLANATION OF FIGURES, PAGES 286, 287.

Fig. 1 represents a diagrammatic transverse section through a typical body segment, and shows the distribution of a segmental spinal nerve. *Sp.C.*, spinal cord; *No*, notochord; *Ao*, aorta; *A.C.*, alimentary canal; *Co.*, cœlom; *G*, ganglion and dorsal root of spinal nerve; *A*, ventral root; I, superior primary division, supplying the dorsal third of the somite; II, somatic branch of inferior primary division, dividing into lateral (*A*) and ventral (*B*) branches, supplying the lateral and ventral thirds respectively; II′, splanchnic branch, connected with a sympathetic ganglion (*Sy*).

Fig. 2 represents the distribution of a similar segmental spinal nerve in a diagrammatic section across the trunk and limb-bud, and shows the latter (*L*) as an outgrowth from the lateral and ventral

thirds of the somite, with the lateral and ventral branches of the nerve (*A* and *B*) distributed to the limb as the dorsal and ventral cords of the limb-plexus.

Fig. 3 represents a similar somite, and shows the homologies of the limb and its nerves, when the latter are considered as representing the lateral branches only. The lateral branch (*A*) is alone supplying the limb-bud; which is shown (hypothetically) as an outgrowth from the "lateral line" of the body (the lateral third of the somite). The ventral branch of the nerve (*B*) is shown passing to the ventral third of the somite.

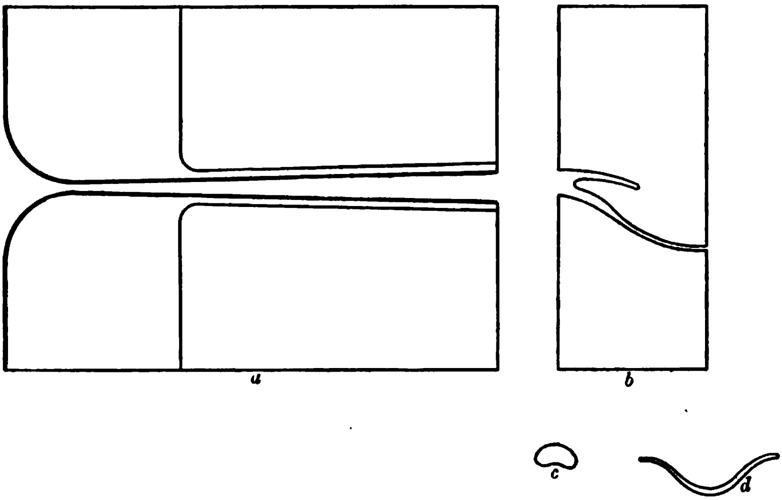
THE EXTERNAL AURICULAR OPENING AND THE EXTERNAL AUDITORY MEATUS IN THE GREENLAND-RIGHT WHALE, *BALÆNA MYSTICETUS.*

By Robert Gray, *Student of Anatomy, University of Edinburgh.*

That the external opening of the ear is remarkable for its small size in the Cetaceans may be held as a general rule, and in this respect *Balæna mysticetus* presents no exception. Indeed, so exceedingly minute and difficult to find is this opening in the Greenland-right whale, especially as it appears in adults, that for long it escaped the observation even of Scoresby, who was so familiarly acquainted with the animal. In his *Account of the Arctic Regions* (published in 1820, vol. i. p. 456), this writer states that "the whale has no external ears, nor can any orifice for the admission of sound be discovered until the skin is removed." In his *Journal of a Voyage to the Northern Whale Fishery in* 1822, p. 154, he, however, states that he has found "the external openings of the ear to be one-sixth of an inch in diameter in a 19-feet long sucker." Eschricht and Reinhardt, in their *Memoir on Balæna mysticetus*, p. 154, state that "the external orifices of the ear were found in the new-born whale (a sucker 13 feet long) to be 9 inches and 6 lines behind, and 1 inch 7 lines below the eyes; they were almost circular, and about 2 lines in diameter." In an 8-feet long fœtus which they examined, "the orifices of the ear were found to be only 3 inches behind the eyes, and 1 inch higher than a horizontal line supposed to be drawn from the fissures between the eyelids in a backward direction." They also state, concerning the orifices of the ear of a full-grown whale, pieces of the skin showing which they received, that "they were so small that only a very fine probe could be introduced through them."

During the course of a number of voyages to the Greenland whale fishing I enjoyed abundant opportunity of studying the external characters of *mysticetus*, and the position of the exter-

nal opening of the ear frequently occupied my attention. In a number of whales which I had hitherto examined, I failed to find any trace of the opening externally; but frequently, while the process of making off, *i.e.*, the operation of cutting up the blubber into thin slices, was going on on board the vessel, I secured pieces of the blubber with the external auricular canal exposed in section; but unfortunately in every case the skin had been removed, so that it was impossible to say whether the meatus had opened externally or ended blindly in the integument. This year (1888), however, in a young male, measuring 40 feet 6 inches in length, situated 16 inches behind and a very little below a line drawn horizontally backwards from the posterior canthus of the eye, I succeeded in discovering the opening of the ear, exceedingly minute, and very liable to escape detection. The orifice, which is just sufficiently large to admit the point of a pencil, was situated at the bottom of a slight depression.



Owing to the fact that the whale was partially submerged in the water, I was unable, beyond removing a superficial layer of blubber 6 inches in thickness, to carry the dissection deeper. Afterwards, however, while the process of "making off" already referred to was going on, I made careful search, and eventually succeeded in securing a piece of blubber pierced by the meatus. The canal, at first circular or somewhat oval, increased slightly

in diameter immediately under the skin, then ran onwards unchanged until reaching the deeper part of the blubber, when it became semicircular; and then, expanding suddenly, increased greatly in width, the space formed being filled by an outgrowth of the walls. This structure, which appeared to consist entirely of adipose tissue, was conical in form, the apex of the cone being directed outwards, accurately filling the interior of the meatus, and undoubtedly performing the function of a valve, preventing the access of water to the ear while the animal is submerged. Beyond this I was unable to trace the course of the canal, the blubber having been removed from the subjacent parts, nor, unfortunately, did we succeed in capturing another whale during the voyage.

EXPLANATION OF FIGURE, PAGE 301.

The figure, which is somewhat diagrammatic, represents, natural size, a section through the skin and blubber, showing the minute orifice of the ear expanding on the one hand towards the surface, more gradually on the other as the meatus proceeds towards the ear. The two parts of the figure (*a*) and (*b*) are left ununited, the distance between them not having been determined. The blubber in this region is very thick—it may be many inches. The meatus, at first circular, assumes before the valve is reached a crescentic form, represented by (*c*); at the deepest part of the dissection it has greatly increased in size, represented by (*d*), the base of the valve being shown. The space enclosed between the double lines in (*a*) represents the epidermis prolonged inwards as a lining to the meatus, but greatly decreased in thickness; in (*b*) it is too thin to be represented by a double line.

THE MUSCULUS STERNALIS AND ITS NERVE-SUPPLY. By FRANCIS J. SHEPHERD, M.D., *Professor of Anatomy in M'Gill University, Montreal.*

THE subject of the musculus sternalis and its nerve-supply has been so exhaustively treated by Professor Cunningham of Dublin in a recent number of the *Journal*[1] that it would appear superfluous for me to add anything further, had not Professor Bardeleben[2] of Jena still more recently recorded twelve additional cases of the musculus sternalis observed by him since 1876. In this paper he states that, in every case in which the nerve-supply was traced, it came from the intercostals (generally from the 3rd and 4th), and he seems to doubt the possibility of the true "sternalis" muscle receiving its innervation from the anterior thoracic. Thus it appears that there is still a considerable difference of opinion regarding the nerve-supply of this very puzzling muscle, and for this reason I wish to place on record three additional cases in which the nerve-supply was traced. Professor Bardeleben makes no reference in his paper to the observations of Professor Cunningham and others on this subject. It seems strange that the observations of anatomists, other than German, should have been overlooked or disregarded, especially as the number of cases reported by Dr Cunningham, where the nerve-supply was traced to the anterior thoracic nerves, far exceeded in number those recorded by Professor Bardeleben.

In vol. xix. of this *Journal*[3] I published a paper on the occurrence of the musculus sternalis in anencephalous monsters, and stated that I had found nine muscles in six fœtuses; in six the nerve-supply was traced to the anterior thoracic, in one to the anterior thoracic and intercostal, and in two it could not be made out. Since the publication of that paper I have examined three anencephalous fœtuses and one cyclopean. In one anen-

[1] Vol. xxii. p. 392.

[2] *Anatomischer Anzeiger*, May 1888, Nos. 11 and 12.

[3] P. 311.

cephalous fœtus, a male, no sternalis muscle was found, nor was any found in the cyclopean; but in the other two, both females, three well-developed "sternalis" muscles existed. This makes a total of twelve "sternalis" muscles observed in nine anencephalous fœtuses, and in ten of these muscles the nerve-supply was traced.

CASE VII.[1]—*Female fœtus, anencephalous, with spina bifida in cervical region. Musculus sternalis bilateral. Great pectoral of each side deficient. Nerve-supply from internal anterior thoracic.*

On both sides the muscle is of large size. The *right* muscle is continuous above with the sterno-mastoid, and arises from the first piece of the sternum in common with the great pectoral. It passes downwards and outwards, expanding into a large, flat muscle which is inserted into the 5th, 6th, and 7th ribs immediately external to their cartilages. The most external fibres of the muscle are blended with the lower portion of the great pectoral, while the innermost fibres continue down over the pectoral muscle to end in the aponeurosis of the external oblique muscle. The central portion of the great pectoral which arises from the costal cartilages of the 2nd, 3rd, and 4th ribs is absent, so that a triangular interspace of considerable size is left between the existent upper and lower portions of the pectoralis major; in this interspace a nerve is readily found which reaches the "sternalis" about its middle, and supplies it by piercing its under surface. On tracing back this nerve it is seen to be branchless until it reaches the upper border of the lesser pectoral, where it joins the internal anterior thoracic, and gives a branch of considerable size to the lower portion of the great pectoral. None of the intercostal nerves can be traced to the "sternalis;" they are seen to loop around the inner border of the muscle, but do not pierce or supply it.

The *left* muscle is also of large size, but more fusiform in shape and more oblique in direction. It is attached above to the second piece of the sternum; having an origin in common with the great pectoral, it passes downwards and outwards over the lower portion of that muscle and ends in the aponeurosis of the external abdominal oblique. A much larger portion of the

[1] These cases are numbered consecutively with those recorded in vol. xix.

great pectoral is deficient than on the opposite side, and in this interspace is seen a long branchless nerve coursing towards the "sternalis" muscle and supplying it from its outer surface. This nerve has exactly the same course and distribution as its fellow of the opposite side, and is a branch of the internal anterior thoracic. The intercostals recur around the inner border of the muscle, but do not pierce or supply it.

In those cases where the great pectoral is deficient I can now, with the greatest ease, find the nerve supplying the sternalis; it is always in the same situation, in the interspace between the upper and lower portions of the great pectoral.

CASE VIII.—*Anencephalous Female Fœtus; spina bifida in the cervical region. Hare-lip. Musculus sternalis unilateral. No deficiency in the great pectoral. Nerve-supply from both the internal anterior thoracic and the intercostal* (see fig. 1).

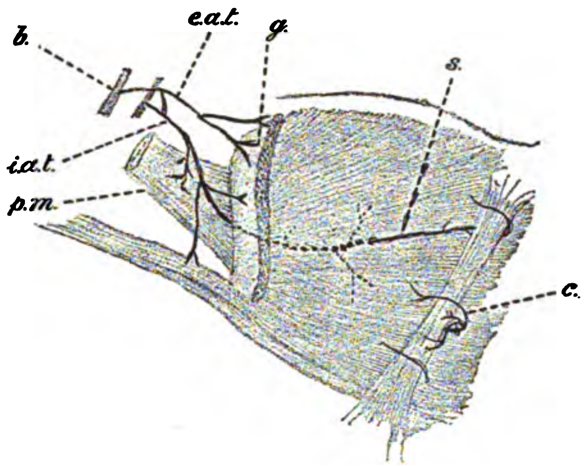


FIG. 1.—Single sternalis of left side. *b.*, inner cord of brachial plexus; *c.*, 3rd intercostal nerve sending branch to muscle; *s.*, branch of internal anterior thoracic piercing pectoral muscle, and also going to sternalis; *e.a.t.* and *i.a.t.*, external and internal anterior thoracic nerves; *g.*, upper part of great pectoral muscle; *p.m.*, pectoralis minor.

On the left side is a well-marked "sternalis" muscle. The muscle is ribbon-shaped and of no great size, but quite distinct. Above it is attached to the lower part of the first piece of the sternum by a fibrous origin; it soon becomes muscular, and

continues in a downward and outward direction over the great pectoral and a little outside the sternum, to become lost in the abdominal aponeurosis. The muscle is in no way connected with the great pectoral. A small, slender nerve is seen piercing the great pectoral about its middle, and on a level with the upper border of the third rib; it passes upwards and inwards to the upper part of the sternalis, which it supplies from the under surface. When traced back, this nerve is seen to come from the internal anterior thoracic; before it pierces the pectoralis margin it gives off several branches to that muscle. The internal anterior thoracic, when dissected out, has the following course:—After being given off from the inner cord it passes inwards, and is joined by a branch from the external; before piercing the costocoracoid membrane it gives off a large branch to the lesser pectoral; it then passes over the lesser pectoral, giving branches to lower part of the great pectoral, as it proceeds inwards between the great and lesser pectorals; before piercing the great pectoral, and while in the substance of that muscle, it gives off numerous branches of supply, and then proceeds inwards to supply the "sternalis." On examining the intercostal nerves, the third is seen to pass under the "sternalis," and to hook around the inner edge; as it does so it gives off a large branch of supply to the lower part of the "sternalis." None of the other intercostals are distributed to the sternalis.

As I mentioned above, I have now traced the nerve-supply to ten of these muscles, occurring in anencephalous fœtuses, with the following result:—*All* were supplied by the anterior thoracic; two muscles also received an additional supply from the intercostals. Now, in every case where the great pectoral was deficient, the nerve supply was derived from the anterior thoracic nerves alone; and in the only two cases in which the "sternalis" occurred without deficiency of the great pectoral the muscle had a double nerve supply, viz., from the anterior thoracic and intercostals. This almost seems to indicate that there are two different kinds of "sternalis" muscles. Bardeleben[1] holds that, excluding those cases of so-called "sternalis" which belong to the platysma or pectoral varieties, we have left the "typical sternalis," which usually extends from the rectus sheath

[1] *Loc. cit.*

to the sterno-mastoid, and belongs to the muscular system of the rectus abdominis and pubo-hyoideus, and derives its nerve-supply from the intercostals. He suggests that it should be called the "*rectus abdominis superficialis.*" In my cases the muscles supplied by the intercostals also received a special nerve-supply from the anterior thoracic. This would seem to point to a form of sternalis intermediate between those supplied on the one hand altogether by the anterior thoracic, and on the other by the intercostals.[1]

I do not think that any one who has seen in the anencephalous fœtus a well-marked specimen of the "sternalis" muscle, accompanied by deficiency of the great pectoral, could for a moment doubt that it was the missing portion of the pectoral, which had become displaced or rotated, even if he were ignorant of its nerve-supply. In those cases, however, where there is no deficiency of the great pectoral, and where the sternalis muscle is quite superficial and unconnected in any way with the great pectoral, the case is not so clear, especially if the nerve-supply be partly or wholly (as in the cases reported by Professor Bardeleben) derived from the intercostals. I confess that in these cases my ideas as to the homology of the sternalis are not at all settled. Perhaps a wider knowledge of the myology of the various animals will in the future throw some fresh light on the subject. The occurrence of this muscle so commonly in anencephalous monsters would rather point to its being a reversion, and not a new muscle appearing in man.

[1] I have, however, never yet been fortunate enough to meet with a "sternalis" muscle altogether supplied by the intercostals, and I imagine, if the branch from the anterior thoracic were looked for carefully, it would always be found.

ON SOME POINTS IN THE ANATOMY OF A *MEGAPTERA LONGIMANA*. By JOHN STRUTHERS, M.D., *Professor of Anatomy in the University of Aberdeen.*

(*Continued from vol. xxiii. page 163.*)

PART IV.

THE SKULL.

The following table of measurements, besides showing the size and proportions of the various parts of the skull of this Megaptera, will enable these to be compared with the corresponding parts of B. musculus. The measurements to which an * are prefixed are those given in the same order by Professor Flower (*Proc. Zool. Soc.*, 1864, p. 411) of several skulls of B. musculus, with which the sizes in the second column of my table may be compared. Some of the measurements given in the table may seem unnecessary, but they may be useful in the study of the skull in fin-whales. In making the measurements and the observations which follow, I had the skulls of the Megaptera and the B. musculus placed together, so that they could be approached on all sides and studied comparatively.

1. TABLE I.—*Measurements of the Skull*, given in inches.

	Megaptera, 40 feet long.	B. musculus, 50 feet long.
*1. Length of skull, in straight line, to point of upper jaw, ...	125	145
*2. Breadth of condyles, ...	12⅛	11¾
3. Condyle, height, ...	9½	10
4. ,, breadth, ...	5¼	5⅝
5. Projection of condyles behind most projecting part of exoccipitals, ...	2¼	1¼
6. Projection of condyles behind bone immediately external to them, ...	3	4
7. Depth of depression between condyles and between posterior part of exoccipitals, .	2¼	3½
8. Depth of supra-occipital depression, . .	3½	2¾
9. Foramen magnum, height, ...	4⅞	4½
10. ,, width, ...	4⅝	4
*11. Breadth of exoccipitals, ...	41½	43
12. Descent of exoccipitals below level of condyles, .	3½	2
13. From exoccipital to outer edge of squamosal, horizontally out, ...	15	12
14. Descent of squamosals below level of condyles,	14	10
*15. Breadth of skull (greatest) at zygoma of squamosals, ...	71¼	66⅛
16. Ditto near posterior angle of zygoma, . .	60	58
*17. Length of supra-occipital, . . .	29	31
18. Length of articular process of squamosal (zygoma), ...	22½	27½
19. Malar, length of outer border, straight, .	8	8¼
20. Ditto, breadth at narrowest part, . .	2⅝	1⅛
21. Outer edge of orbit, length, ...	9	9
22. ,, ,, height, ...	8	7
23. Temporal passage, width at front, . . .	20	19
24. ,, antero-posteriorly, greatest,	8¼	10½
25. Temporal fossa, transversely, greatest, . .	31	28
26. ,, antero-posteriorly, . .	34	42
27. ,, greatest depth, . .	10½	10¾
28. ,, anterior edge anterior to peak of nasals, . . .	½	10½
29. ,, posterior edge to posterior border, . . .		
30. ,, of squamosal (sagittal), .	18	15
*31. Orbital plate of frontal, transversely, greatest,	31	27
*32. ,, ant-post., at inner part, . .	27	29
*33. ,, ,, at outer part, upper surface, . . .	12	15½
34. ,, supra-orbital edge, straight, .	8	10
*35. Nasals, length, inner border, ...	9½	7½
36. ,, ,, outer border, ...	9⅝	10¾
*37. ,, breadth of the two, at posterior end, .	4¼	5⅝
*38. ,, ,, at anterior end of outer border, .	10¼	10½
39. ,, ,, at where inner border ceases, .	10¼	8½
40, 41. ,, breadth of each at middle of inner border, upper surface, . .	1½	3¼

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6. Projection of condyles behind bone immediately external to them,	3	4
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8. Depth of supra-occipital depression,	3½	2¾
9. Foramen magnum, height,	4⅞	4½
10. ,, width,	4⅝	4
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19. Malar, length of outer border, straight,	8	8¼
20. Ditto, breadth at narrowest part,	2⅝	1⅛
21. Outer edge of orbit, length,	9	9
22. ,, ,, height,	8	7
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*31. Orbital plate of frontal, transversely, greatest,	31	27
*32. ,, ant-post., at inner part,	27	29
*33. ,, ,, at outer part, upper surface,	12	15½
34. ,, supra-orbital edge, straight,	8	10
*35. Nasals, length, inner border,	9½	7½
36. ,, ,, outer border,	9⅝	10¾
*37. ,, breadth of the two, at posterior end,	4¼	5⅝
*38. ,, ,, at anterior end of outer border,	10¼	10½
39. ,, ,, at where inner border ceases,	10¼	8½
40, 41. ,, breadth of each at middle of inner border, upper surface,	1½	3¼

TABLE I.—*Measurements of the Skull*—continued.

	Megaptera, 40 feet long.	B. musculus, 50 feet long.
42. Nasals, greatest thickness, between upper and under surfaces, . . .	8	9
43. ,, width of depression between nasals, .	1½	⅞
44. Smallest breadth between temporal fossæ, across nasals, ...	10⅝	15½
45. Length of cranium, straight from end of occipital condyle to anterior end of nasal, .	39	38
46. Ditto, ditto, to anterior edge of temporal fossa,	40	49
47. Ditto, ditto, to transverse frontal fossa, . .	32	32½
*48. Length of beak, from anterior edge of temporal fossa, ...	85	96
49. Ditto, from transverse frontal fossa, . .	94	112½
*50. Projection of premaxillary beyond maxillary, .	6	8
51. Length of maxillary, from end of frontal process, ...	89½	108
52. Ditto, from curved border at temporal fossa, .	78½	89
53. Ditto, from back part of ant.-orbital angle, .	94	102
54. Ditto, on palatal surface, . . .	96	107
*55. Breadth of maxillaries at hinder end, . .	18	17
*56. Ditto, across orbital processes, on the curve, .	80	70
*57. Breadth of beak at base, on the curve (just before anterior edge of temporal fossa), .	45	48
58. Ditto, straight, by callipers, . . .	38¼	40
*59. Breadth of maxillary at same, . . .	16	16¾
*60. ,, of premaxillary at same, . .	1½	0
61. ,, of mesial gap at same, . . .	9½	13½
*62. Breadth of beak, ¼ of its length from the base, on the curve, ...	33½	36
63. Ditto, straight, by callipers, . . .	31¼	33⅝
*64. Breadth of maxillary at same, . . .	8½	12
*65 ,, of premaxillary at same, . .	4	4¾
66. ,, of mesial gap at same, . . .	8½	2¼
*67. Breadth of beak at middle, on the curve, .	27½	27
68. Ditto, straight, by callipers, . . .	26¼	26
*69. Breadth of maxillary at same, . . .	8¼	8½
*70. ,, of premaxillary at same, . .	4¼	4⅜
71. ,, of mesial gap at same, . . .	3	1⅛
*72. Breadth of beak at ¾ of its length from base, on the curve, ...	19¼	17
73. Ditto, straight, by callipers, . . .	18½	16½
*74. Breadth of maxillary at same, . . .	4½	3½
*75. ,, of premaxillary at same, . .	3⅞	4
*76. ,, of mesial gap, ...	2½	1¾
77. Premaxillary, length, ...	92	113
78. ,, breadth where maxillary ceases distally, . . .	3⅜	3⅝
79. Prenasal gap, greatest width, . . .	14½	12½
80. ,, length, from anterior border of nasals,	31½	25
81. Length of narrow intermaxillary space, from prenasal gap to end of beak, . . .	55	84
82. Vomer, length, ...	90	121
83. ,, greatest depth of its cavity, . .	8¾	8½
84. ,, greatest width of its cavity, . .	7⅜	6⅝

TABLE I.—*Measurements of the Skull*—continued.

	Megaptera, 40 feet long.	B. musculus, 50 feet long.
85. Palate bone, length, ...	24	25¼
86. ,, greatest breadth, . . .	10½	10½
87. Maxillary, on palatal aspect, breadth at base, straight, ...	20½	21
88. Maxillary, greatest depth of concavity there, .	5¾	8¼
89. ,, breadth at ¼ of its length from base,	18	18
90. ,, greatest depth of concavity there, .	4½	6⅛
91. ,, breadth at middle, . . .	14	14
92. ,, greatest depth of concavity there, .	3⅛	3⅝
93. ,, breadth at ¾ of its length from base,	9¾	9¼
94. ,, greatest depth of concavity there, .	1⅝	1⅞
95. Cranial cavity, length from lower edge of foramen magnum to edge of olfactory fossa, . . .	12	16
96. ,, greatest breadth (at temporal fossa), . . .	18	16
97. ,, greatest height (at sella turcica), . . .	8	8
98. Olfactory fossa, length, . . .	4	5
99. ,, breadth, at entrance, . .	3	3¼
100. ,, height, at entrance, . .	2	3

2. LENGTH AND PROPORTIONS OF THE SKULL.—The length of the skull, taken to the point of the upper jaw, is less than that given as the length of the head (Table I. Part III.), by the amount of projection of the mandible beyond the beak and of the soft parts in front of the mandible. The amount to which the condyles project behind the rest of the skull falls to be deducted in estimating how much the head forms of the total length. The comparison of the parts in the two skulls in the following observations is between the actual sizes, but it is to be borne in mind that the Megaptera was 40 feet long, the skull 125 inches in length, the B. musculus 50 feet long, the skull 145 inches in length. In the true comparison of the lengths of the several parts of the skulls, therefore, about a seventh has to be deducted from those of B. musculus, or a sixth added to those of Megaptera. In like manner the comparison of the actual breadths does not bring out the full proportionate breadths in Megaptera, unless it is borne in mind that the skull of Megaptera was only 125 inches in length and that of B. musculus 145.

3. OCCIPITAL BONE AND REGION.—The *foramen magnum*

is larger in Megaptera than in B. musculus, and broader in proportion to its height (see measurements in the Table). At the upper part of the foramen the bone is thin in Megaptera (not a ¼ inch), in B. musculus very thick (2 inches).

Condyles.—The condyle is narrower in Megaptera, but the two condyles together are wider in Megaptera owing to the greater width of the intercondyloid space. In B. musculus the lower end of the foramen magnum joins a narrow intercondyloid triangle (1 inch wide) at an acute angle; in Megaptera the angle is obtuse, and the upper part of the intercondyloid space is a wide triangle (3 inches wide, 2 in length). The space below this is not roofed over in Megaptera, but is so in B. musculus. In Megaptera the condyles begin above by a non-articular ridge 2 inches in length, beginning 1 inch above the foramen; in B. musculus the articular condyle begins at once, and on a level with the top of the foramen. The condyle is more bent vertically in Megaptera. The *projection of the condyles* beyond the rest of the back of the skull[1] is greatest in Megaptera, but their projection from the level of the bone immediately external to them is 1 inch more in B. musculus than in Megaptera. This will allow greater freedom and extent of motion in B. musculus.

Supra-occipital.—In B. musculus there is a very well-marked sharp median ridge, rising to an inch in height, ending behind in a sharp diamond-shaped tuberosity, 7 inches from the foramen magnum. This ridge is very obscurely marked in Megaptera, which presents a broad deep median hollow along the whole length of the bone, bounded on each side by the smoothly convex side of the bone. In B. musculus these parts have irregular muscular markings, and the hollow is less. The upper end of the supra-occipital, at the transverse frontal fossa, is narrower in Megaptera (10 inches) than in B. musculus (14 inches).

The *ex-occipitals* are not so broad in Megaptera as in B. musculus, and are smoothly convex in both directions from a little way external to the condyles; the most projecting part is at the junction of the outer and middle thirds, from which the surface falls smoothly to the outer edge, without any par-occipital ridge. In B. musculus there is a transverse depres-

[1] This projection does not occur at all in B. borealis or in B. rostrata.

sion along the outer half, the surface more sharply bent vertically and flatter transversely; the most projecting part is at the extreme outer edge, rising into a prominent par-occipital ridge. The ex-occipitals descend below the level of the condyles more in Megaptera (3½ inches) than in B. musculus (2 inches).

Basi-occipital.—In Megaptera the sub-occipital notch between the inner walls of the ear-bone spaces, and receiving the vomer, is wider in Megaptera (15 inches, in B. musculus 13). This part will be further noticed with the vomer. External to this, the sharp triangular fissure in the occipital margin, opening into the ear-bone space, is much deeper and wider in Megaptera (depth 4 to 5 inches in Megaptera, in B. musculus 2 inches).

Occipital Plate of the Temporal Bone.—This plate, in its form and great size, presents one of the most striking differences between Megaptera and B. musculus. Its outer and lower part (post-mandibular process) has the glenoid fossa in front for the support of the condyle of the mandible. It is much larger and more square-shaped in Megaptera. The measurements are, along lower border, sloping downwards and outwards, in Megaptera 13 inches, in B. musculus 12; transversely at about the middle, outer border moderately concave, Megaptera 15, B. musculus 12; transversely at posterior angle of temporal fossa, in Megaptera 18½, in B. musculus 13½; antero-posteriorly, at inner part, in Megaptera 18, in B. musculus 14½; at outer border, in Megaptera 23 (going as far as the articulation with the frontal bone and to four inches from the anterior end of the zygoma), in B. musculus, as seen from behind, also about 23, but indefinite from the rounding off into the long zygoma, and about 11 inches from the anterior end of the zygoma. The outward slope of this border is such that its upper part is more external than its lower, in Megaptera 7 inches, in B. musculus 2½. The upper border, going outwards, slopes in Megaptera a little downwards, in B. musculus very much upwards. The more square form in Megaptera is mainly owing to the greater height at the inner part, from the temporal fossa cutting less back into it, and to the greater general breadth.

4. Temporal Fossa and Passage.—When these skulls are viewed anatomically, from above as well as from the side, it is seen that the parts connected with the temporal muscle present

the most marked of all the characters which differentiate the skull of Megaptera. Considering the enormous length of the mandible in whalebone whales, and its weight even in the water, we would expect to find a correspondingly large temporal fossa and passage, and, as the head is flat, that the fossa would assume an expanded form.

From the measurements given in the table, it is seen that the *temporal fossa* is broader by 3 inches in the Megaptera, and longer by 8 inches in B. musculus, and is of nearly the same depth in each, at the deepest part, which is towards the back part of the inner side. From 5 to 6 inches of the greater length in B. musculus is obtained by an angular prolongation behind where the zygoma and squame of the temporal meet, while in Megaptera the posterior border is uniformly concave. The great difference, however, is in the shortness of the fossa at its outer compared with its inner part, being in Megaptera scarcely half as long externally as it is internally. This is owing to the well-known obliquity backwards of the orbital process of the maxillary and of the anterior border of the orbital plate of the frontal, so that at the outer part that plate is but 12 inches in length, as compared with 27 internally, two of the 27 covered by the maxillary at the anterior end of the fossa. In B. musculus the obliquity is very much less, the measurements at the corresponding parts being respectively 15½ and 29 inches; but about 4 inches of this narrowing is obtained by a forward direction of the posterior border of the plate, while the posterior border of the plate in Megaptera is, on the contrary, directed a little backwards. The less length of the temporal fossa, and its farther back position on the skull, in Megaptera are made manifest by observing its relation to the ends of the maxillary and nasal bones. A line drawn across the skull where the maxillary and supra-occipital bones come in near relation (the transverse frontal fossa), has in front of it, in Megaptera less than a third of the length of the temporal fossa (9 to 10 inches), only its narrow anterior end, and passes at about 3 to 4 inches in front of the orbit; while in B. musculus well on to half of the fossa (18 inches) is in front of the line, and it passes across the posterior end of the orbit. In relation to the nasal bones, the anterior boundary of

the temporal fossa reaches, in Megaptera to only ½ inch in front of the median peak of their anterior ends, in B. musculus to 10½ inches. A difference is seen also in the level of the floor of the fossa, especially on the outer half of the frontal plate, which in Megaptera is convex with a general fall backwards (except at the anterior angle), while in B. musculus it is flat with a slight fall forwards. Standing behind the skull, with the eye on a level with the upper border of the occipital plate of the temporal bone, there is seen above it, in B. musculus only the inner part of the anterior end of the temporal fossa; in Megaptera the fossa, with its great slope, is seen in its whole length, and the outer half of the posterior border is also seen.

The differences in the temporal fossa in Megaptera and B. musculus appear to be mainly owing to the greater breadth of the cranium in Megaptera, in adaptation to a wider mandible requiring the post-mandibular plate of the occipital to be not only farther out but also farther back.

Temporal Passage.—This large aperture, leading down from the back part of the temporal fossa upon the condyle or neck of the mandible, is a continuation of the temporal fossa, but may be conveniently distinguished by the above name. It is large enough to allow a man's body to pass. In Megaptera the posterior wall is uniformly and smoothly concave, with a depth of 10 inches at the middle, and but faintly marked off from the glenoid surface below, both being nearly vertical. In B. musculus there is a well-marked angle in the posterior wall; the depth at the middle is 7 inches, and the wall here is marked off from the glenoid surface by a strongly pronounced transverse ridge, towards which both surfaces slope forwards. The angle on the posterior wall gives the passage a triangular form in B. musculus contrasting with the semilunar form in Megaptera.

The *anterior boundary* of the temporal passage is formed by the thick posterior border of the supra-orbital plate of the frontal bone, rounded by the bone turning downwards and forwards like a scroll, bounding the orbital cone posteriorly, and forming a pulley-surface for the play of the temporal muscle. In Megaptera it is directed a little backwards, with slight con-

cavity; in B. musculus it slopes forwards in its whole length. (Thickness at the inner, middle, and outer parts, in Megaptera 6, 3½, and 2 inches; in B. musculus, 5, 3, and 1½.) The direction of this great post-orbital bar is determined by, or determines, the direction of the orbit.[1]

5 Differences of the Bones forming the Temporal Fossa and Passage.—The bones to be noticed here are the parietal, at the fossa and passage, and behind and below the orbital cone; at the inner part of the passage, the temporal, sphenoid, and pterygoid; below the passage, the pterygoid, temporal, and palate; and, behind and below the orbital cone, the pterygoid as well as the parietal.

The *parietal* bone has much greater expansion on the fossa in Megaptera than in B. musculus, covers the inner wall as far forwards as to about 3 to 4 inches from the anterior edge of the fossa, and extends outwards on the floor to a breadth of from 6 inches at the middle of the fossa to 8 inches at the bar, and out upon the back of the bar for 13 inches as a thin lamina. In B. musculus it covers only the inner wall, forwards to within about 6 inches of the anterior edge of the fossa, none of the floor, and does not reach out on the bar. Where the bar is covered by the parietal in Megaptera, it is rough in B. musculus, along fully its inner half, and was in the recent state covered by cartilage. The parietal is seen to cease by a natural edge 1 inch internal to this rough part. On the posterior wall of the temporal fossa and passage, the parietal goes outwards farther in B. musculus than in Megaptera (10 inches, in Megaptera 7 to 8); the descending parieto-temporal suture curves differently, its outward projection in B. musculus much greater above than below, in Megaptera greater below than above; the border then sweeping forwards in B. musculus to reach the level of the top of the sphenoid, in Megaptera down to the level of the top of the pterygoid.

The *temporal* bone here is divided for some way into two

[1] In this connection it is interesting to note the different direction of this great bar in the different Finners. Its direction in Megaptera and in B. musculus is noted above. In B. borealis it is directed considerably backwards, giving the supra-orbital plate great breadth externally and its square form. In B. rostrata still more backwards, giving a rhomboid plate.

parts by a suture-like fissure, passing upwards and backwards. The lower part, much the broadest, articulates with the pterygoid in both to about the same extent, but is smaller above in B. musculus than in Megaptera (3 inches at the middle, Megaptera 4½), and the fissure in B. musculus runs into the angular recess of the wall and then bends sharply down. The form of the upper part is determined by the relation to the parietal; in Megaptera broad above, tapering below like a sickle, its point just reaching the top of the pterygoid; in B. musculus its continuation downwards is as broad as the hand, reaching forwards to articulate with the pterygoid for 3 inches and with the base of the sphenoid wedge.

The *sphenoid* bone shows itself on the surface here in B. musculus, but not in Megaptera. In B. musculus it has the form of a narrow wedge, 6 inches in length; height of base, posteriorly, 1 inch, tapering forwards to a sharp point at the root of the orbital cone. It articulates posteriorly with the temporal, above with the parietal, below with the pterygoid. It and the parietal are seen to end at the same point together at the root of the orbital cone. The parietal is thus cut off from reaching any part of the pterygoid, by the interposition of the sphenoid, in contrast with the condition in Megaptera.[1]

[1] The sphenoid shows itself here in B. borealis and also in B. rostrata, but does not cut off the parietal from meeting the pterygoid. In *B. borealis* it is wedge-shaped, shortened behind, so that the parietal meets the pterygoid behind it for 2 inches. The temporal is thus cut off from meeting the sphenoid, but its part above the fissure meets the pterygoid for 1½ inch. In *B. rostrata* the sphenoid here is 1 inch in length on the right side, 1⅝ on the left, and about ½ inch in height, the wedge shortened in front so that the parietal meets the pterygoid in front of the sphenoid for 1½ to 1¾ inch. The tongue-like process of the temporal meets the posterior end of the sphenoid, and below that the pterygoid. It might seem that the concealment, or exclusion, of this part of the post-sphenoid here in Megaptera was owing to the parietal having to reach out on the pedicle of the orbital cone, but in B. borealis the parietal reaches out below the cone for 3 inches beyond the first inch occupied by the pterygoid, and far enough forwards to cover the fissure between the two scrolls. Again, that it is not the backward direction of the post-orbital bar that determines the extension of the parietal upon it in Megaptera, is seen by the fact that the backward direction of the bar is greater in B. borealis than in Megaptera, but the parietal does not extend on the back of the bar, which is rough there, as in B. musculus, though not so rough. In B. rostrata the backward direction of the bar is still greater than in B. borealis, but the parietal does not reach over any part of it, and the fissure between the two scrolls of the orbital cone is widely open from the root.

The *pterygoid* bone, as seen here, is in B. musculus square shaped, 6 inches in height, 4 in breadth, directed upwards and backwards; in Megaptera rather triangular, 4 inches in height, 2 to 2½ inches in breadth, directed very obliquely backwards and upwards. In Megaptera it is only on the right side that its narrow apex is actually touched by the sickle-like part of the temporal, on the left side there is an interval of ¾ inch. In Megaptera this temporal aspect of the pterygoid is marked off sharply, at about a right angle, from the basilar aspect, while in B. musculus the surface is continued down in a much more rounded form. Here the lower division of the temporal is seen to send forwards a process across the pterygoid, just below the root of the orbital pedicle, in Megaptera to within about 1 inch from the palate bone; in B. musculus the interval, at the narrowest, at the foramen, is 2½ inches. The greater convexity of the pterygoid bone here, in B. musculus, is owing to the bulging of the wall of the auditory space. The pterygo-temporal foramen here (admitting two fingers) is modified accordingly, elliptical and oblique in Megaptera (3 inches by nearly 1 inch), the pterygoid bounding only the anterior end; in B. musculus, ovoid, the pterygoid forming the inner half.

The *palate* bone at this region is different. In Megaptera, where the posterior and upper borders meet, it sends up a triangular process to below the root of the orbital pedicle, pushing the pterygoid outwards; upper border of palate bone deeply concave for the first six inches; posterior border concave backwards; foramen between palate, pterygoid, and frontal admits a finger. In B. musculus the palate bone here wants all these characters; the posterior edge is very convex, indeed has a blunt angle above the middle. The foramen is merged in the long and wide palato-maxillary fissure to be noticed with the nasal cavity.[1]

[1] The parts which assist to close the orbital cone below are more conveniently studied with these parts than with the orbit viewed externally. In B. musculus the two curved laminæ alone form the cone all the way in, the posterior scroll, as in all the finners, below the anterior, where they meet and cross for a little. In Megaptera the cone is covered and as if supported below by the following parts, from within outwards. (1) The suborbital process of the temporal bone, above noted as crossing the pterygoid, supports the pterygoid at the base of the pedicle. (2) The angular process of the palate bone supports the pterygoid from before. (3) The pterygoid bone sends a process outwards below the cone for 3 inches; it

6. Malar Bone.—In Megaptera the malar bone is much broader ($2\frac{5}{8}$ inches) along its posterior half than in B. musculus; much more deeply grooved at each end, transversely, to receive the zygoma and maxillary; and its enlargement at the maxillary end (5 inches in breadth, $2\frac{1}{2}$ in length) is abrupt and at right angles to the rest of the bone. In B. musculus the enlargement (4 to 5 inches in length, $3\frac{1}{2}$ in breadth) is more gradual, and is in the direction of the curve of the bone, pushing in below the lachrymal. At the posterior end, in B. musculus, there is an abrupt process, half an inch long, like the end of the little finger, projecting inwards. The outer edge of the malar in B. musculus appears unfinished, as if it had been covered with cartilage.

7. The Orbit.—The opening of the orbit is larger in Megaptera, about the same in length, but greater in height (8 inches, in B. musculus 7). This is owing to the much greater curve of the upper edge of the frontal plate in Megaptera (concavity 3 inches deep, and uniform); in B. musculus there is very little curve on the anterior three-fourths of the frontal edge, the bend down being on the posterior fourth. In front of the orbit, the frontal plate presents the same difference for about a third of its breadth, convex in Megaptera, flat in B. musculus. In the roof of the orbit the same difference in the concavity is seen, back to the mouth of the narrow orbital cone. The mouth of the cone is ovoid, in Megaptera antero-posteriorly, in B. musculus vertically. The meeting of the two laminæ which close the cone below is, from the orbital margin, in Megaptera 13 inches, in B. musculus 15. The plane of the orbital edge is different. Prolonged forwards the plane would, in Megaptera, cut off the anterior $\frac{1}{3}$ or $\frac{1}{4}$ of the beak; in B. musculus it would clear the beak, passing about a foot external to it. It is evident

rises higher and reaches farther out before than behind, rising to the height of the anterior scroll—that is, an ascent of $1\frac{1}{2}$ inch on the pedicle. (4) The parietal bone, external to the pterygoid, covers the cone below for 3 inches. This is to within 5 inches of where the two scrolls diverge and open the cone outwardly. Over these 3 inches the parietal turns well up in front, to as high as the edge of the anterior scroll. The great extension of the parietal on the back of the cone, the post-orbital bar, has been noted above. The two last-mentioned additions give the orbital cone a blunt keel-shape and smooth surface below, in contrast with its flatness and roughness in B. musculus.

to the eye that the orbit has much less obliquity forwards in B. musculus than in Megaptera.

8. Transverse Frontal Fossa.—At the part which may be so named, the supra-occipital, parietals, frontal, nasals, maxillaries, and premaxillaries meet or come in near relation. The anterior edges of the supra-occipital and parietals[1] are seen as two strata lying on the frontal; and, after an interval (the fossa), the frontal meets with the nasals and maxillaries. The gap is 1¾ to 2 inches long in Megaptera, in B. musculus ¾ inch; the depth, ½ to ¾ inch in both. The greater length of the fossa, and its prolongation at the middle, in Megaptera, are mainly owing to the differences at the nasals, to be presently noticed, but the length is the same at the maxillary part as at the top of the nasals. Transversely, the fossa is less in Megaptera than in B. musculus. Here the temporal fossa in Megaptera forms a special inward projection (1 to 1½ inch), gently triangular, as if the skull were pinched at this part, while in B. musculus the inner wall of the fossa goes straight on. The narrowest part between the temporal fossæ is here, at the transverse frontal fossa, in Megaptera 10½ inches, in B. musculus 15½. The great extension of the temporal fossæ inwards in Megaptera, forwards in B. musculus, may in part account for the differences in the nasal bones, especially for their lateral compression behind in Megaptera.

9. Length and Proportions of the Cranium.—The length of the cranium, from the back of the occipital condyles, may be taken to several points. If to the anterior end of the nasals, it is influenced by the very variable nasal bones; if to the anterior

[1] The parietals are not concealed here in any of these skulls. From the usual triangular thickening at the side, where the lateral plate gives off the transverse plate, the latter is seen to pass in to the middle, where, apparently, it is fused with its fellow. In Megaptera the edge of the supra-occipital is about ½ inch thick, but bevelled at the very edge; that of the parietal about ⅙ inch. In B. musculus they are thinner, respectively about ⅓ and ⅛ inch. In B. borealis the edge of the supra-occipital is ¼ to ⅓ inch thick, that of the parietal about ½ inch, and it projects for ½ inch or more in frout of the supra-occipital. The length of the fossa in B. borealis is 1 inch at the maxillaries, 1½ at the nasals. In B. rostrata, too, the parietal edge is seen all the way across. A difference in Megaptera is, that the supra-occipital and parietal bend down a little as they cross, in accordance with the transverse concavity of the supra-occipital, while in these other finners the edges of the supra-occipital and parietal are raised at the middle.

end of the temporal fossa, it is influenced by the muscular arrangements. To the posterior end of the nasal bones is probably the best point. These three measurements are given in the table (Table I. Nos. 45, 46, and 47). Taken at the latter point the length of the cranium is only ½ inch more in B. musculus than in Megaptera (32½ and 32), while in total length the skull in the B. musculus exceeds that of Megaptera by 20 inches (145 and 125). In breadth the cranium of Megaptera exceeds that of B. musculus considerably, at the greatest breadth (measurement No. 15) by 4 to 5 inches (71¼ and 66½). The greatest length and greatest breadth of the skull are, respectively in inches, in Megaptera 125 and 71¼, in the B. musculus 145 and 66½.

10. NASAL BONES.—The nasal bones are very different in Megaptera and B. musculus.[1] The typical form of the nasals in fin-whales is that which the human nasals would present were they thickened towards the nasal cavity until the thickness exceeded the breadth. What would have formed the sixth surface of a four-sided block is reduced to a border by the sloping of the superficial and inferior surfaces to an anterior free border. Differences are seen in the amount of transverse concavity and compression of the superficial surface, in the concavity of the free border, in the separation of the inner borders by a trough-like space or by a process of the frontal, and in the direction of the posterior surface, roofing the fore part of the nasal cavity.

In this *Megaptera* a triangular spine of the frontals, 3 inches long and at first over 2 in breadth, is fitted into the posterior part of the internasal trough, but sunk so as to continue the trough to the top. The visible surface of this frontal spine is

[1] Professor Flower has given (*Proc. Zool. Soc.*, 1864, p. 390) an interesting series of drawings of the superficial surface of the nasal bones. It is not easy to give by one view a satisfactory idea of the form of these bones, to show especially their variously grooved condition. The nasals of this Megaptera differ from his figure (fig. 3) in that their outer margin, at the anterior end, falls short of the inner margin at the peak by only 1 inch (about ⅛ of the whole inner border), and that the triangular space between the nasals runs all the way, tapering to the peak where the two nasals come close together. Compared with his figure (fig. 4) of B. musculus, the outer margins in this B. musculus go much farther forwards, the inner margins form a prominent narrow mesial peak, and at the posterior border the obliquity is in the opposite direction, viz., forwards and outwards, at an angle of 45°.

furrowed, the furrows on each side running backwards and inwards to the mesial suture. No other of these finners has this nasal spine visible on the surface. The trough between the inner borders runs the whole length, on the posterior half 1½ inch wide, 2½ deep, narrowing towards the point where the nasals meet as a prominent peak. The superficial surface is very narrow behind, the first inch like the end of a large thumb, 1¼ inch broad, rounded at the end and sunk into a smoothly arched recess in the frontal. Then the surface broadens by the rapid rise of the inner border, and thereafter becomes grooved and broader distally; breadth at the middle, from edge to edge of the surface, 1½ inch, increased at the hollow of the free border to 3½ inches. On to this point the surface looks more outwards than upwards, the plane of the inner border being about 3 inches higher than that of the outer border. The peak projects fully 2¼ inches beyond the hollow of the distal border; its very oblique inferior border meets the straight superior border at an angle of 45°, the point a little rounded off. The inferior or nasal surface is, on its posterior half, nearly flat with a slight slope upwards to its fellow; on the anterior half, it is bevelled and grooved, facing forwards and inwards, forming a low arched roof, and joins the superficial surface at the free end, the junction so rounded off that there is no exact border between the two surfaces. In this Megaptera there is a foramen in the nasals large enough to receive a large goose-quill, largest in the right nasal, situated on the anterior surface near the distal border. It is present at about the same place in the right nasal only, in this B. musculus.

[In *B. musculus* the proximal end is transverse for ¾ inch close to the middle line, then slopes obliquely outward and forward at an angle of 45°, forming a very jagged articulation with the frontal. This obliquity makes the outer border begin almost 2 inches anterior to the inner. The nasals are at first in close contact and well bevelled up till at about ½ inch from the frontal, the internasal trough begins narrow and shallow (width ⅞ inch behind, narrowing distally, depth ¾ inch) compared with that of Megaptera. External to the sharp and raised inner border is a shallow groove, ¾ inch broad, tapering distally. The superficial surface is broader and more deeply grooved than in Megaptera; from edge to edge at the peak, the depth of the hollow is about 2 inches, in Megaptera about half as much. The greater depth of the concavity on the distal half in B.

musculus is owing to the outer margin not being so low (only 1 inch lower than the inner margin at the peak), and to the surface bending rapidly down to meet the inferior surface. The free border of separation is so far down, and the fall is so rapid, that the distal half of the superficial surface looks almost like a distal surface, like the transversely hollow base of a four-sided pyramid. The two nasals together of B. musculus are not unlike a cocked hat. The peak is as if the distal 2 inches of it in Megaptera had been cut off vertically; its two borders form just a little less than a right angle, and both belong to the superficial surface. A nearly vertical symphysis is thus formed below the peak, about 2½ to 3 inches long, until the sharp distal border is reached which separates the inferior from the superficial surface. The inferior surface is, at the outer part, moderately inclined towards its fellow; on their inner part, rapidly so, making a wedge-shaped recess of the inner part of the roof, 2 inches across, 1½ high.]

These differences between the nasal bones of Megaptera and B. musculus are greater than it is easy to bring out by general measurements or drawings.

11. Posterior Nares.—The form is semilunar, broader at one end, convexity above, the long axis inwards and forwards and a little upwards. The broader end is in Megaptera the inner, in B. musculus the outer. The obliquity is much less in Megaptera, inner end 2 to 3 inches anterior to outer end; in B. musculus 6 inches. They are smaller in Megaptera, long diamater 6 inches; vertically, at outer third 3 inches, at middle 3½, at inner third 3¾. In B. musculus the same measurements are respectively 8½, 4¼, 4½, 4. The width of the posterior nares together, transversly, opposite their anterior ends, is in Megaptera 12½ inches, in B. musculus 14¼ inches.

Parts near the Posterior Nares.—Here there are marked differences. In Megaptera the slanting edge of the *vomer* is shorter (length 8 to 9 inches), and begins close to the posterior end of the bone, as a low ridge, and at the nares it is a 3-inch high septum, and very thin (¼ to ⅜ inch at mid-height there). In B. musculus, instead of a ridge there is a shallow median groove for 3 or 4 inches, running forwards from a 1½-inch-deep median notch, no ridge proper till the nares are reached, when the vomer presents a posterior edge 2 inches in height (2½ on the slanting edge), thickness at mid-height ¾ inch. Length of vomer from posterior end to septum of nares 14 inches, 1½ more at the side of the notch. The alæ of the vomer in Megaptera

go only about a third of the way down on the sides of the great sub-basilar notch, there articulating with the pterygoid by a wavy antero-posterior suture; in B. musculus the alæ go down to within an inch of the lower end of the notch, posteriorly, by a broad triangular plate covering the pterygoid. The sub-basilar notch differs in form in Megaptera, besides being 2 inches broader below, it is broad at the top where it is formed by the vomer, and moderately convex along the sides; in B. musculus it is nearly flat at the top for about 3 inches, and has very little convexity on the sides. The distance of the vomer from the occipital condyle is nearly the same in both (Megaptera 5½ inches, B. musculus 5). The distance from the end of the condyle to the posterior nares, at their septum, shows well the shortness of the cranium here in Megaptera (17½ inches, in B. musculus 24).

The *hamular processes* have been injured in Megaptera, but enough remains to show a marked difference in the broad part. At the notch external to the broad part, the breadth is about the same (Megaptera 4 inches, B. musculus 4½), the difference is in the direction and curvature of the broad part; in Megaptera, directed more inwards and curved inwards, giving a groove on the inner surface into which three fingers may be laid, one behind the other two, while in B. musculus the inner surface is almost flat. This difference accords with the different form of the posterior nares, the outer end of the nares being narrow in Megaptera and broad in B. musculus.

12. Anterior Naris.—There is considerable difference in the form of the single bony anterior naris; in Megaptera compressed vertically, in B. musculus compressed laterally. In Megaptera the outer wall is bent, the whole wall forming a triangular recess about 2 inches deep, and the roof is but moderately arched. In B. musculus the sides are mostly vertical, rounded below, and the roof is much arched, acutely so towards the middle. Width of the space (naturally subdivided into the two anterior nares) in Megaptera 13½ inches, in B. musculus 10 inches; height, from level of upper edge of vomer, in Megaptera about 5 inches, in B. musculus averaging about 5½ inches; height from the floor of the vomer, in Megaptera 13 inches, in B. musculus 12 inches. That would give the anterior nares in B. musculus

as smaller than in Megaptera, although the posterior are larger than in Megaptera. In connection with this, it is to be noted that the blow-hole space in front of the anterior nares is wider in Megaptera than in B. musculus. Also that the cavity of the vomer near the anterior nares is wider as well as deeper in Megaptera; width in Megaptera, inner margin, 7¼ inches, in B. musculus, at the inverted margin 4¾ inches, at the cavity 5½.

13. NASAL CAVITY.—A very marked difference here is in the much larger deficiency of bone in the outer wall in B. musculus, between the palate, maxillary, and frontal. It is best seen when viewed from the anterior naris. The fissure in both goes back to where the frontal forms the anterior scroll of the orbital cone, and opens there. In Megaptera it extends forwards for 11 inches, of which 7 are between the palate and frontal, the remainder in a recess in the hinder end of the nasal plate of the maxillary; height 1 inch, 1½ anteriorly; distance of anterior end from anterior nares 9 inches. In B. musculus the fissure begins at the anterior naris, and as a wide gap, has a length of 17 inches, and a height of 4 inches anteriorly, diminishing backwards to 3 inches. It is entirely palato-frontal, except at the anterior end, where it is bounded by the hinder border of the nasal plate of the maxillary. In Megaptera this plate passes back for 12 inches behind the anterior naris. Seen from the palatal aspect, this fissure in Megaptera, 7 inches in length, 1 to 1½ inch in height, is between the palate bone below and the maxillary and frontal above, the latter after the maxillary terminates at 3 inches from the root of the orbital cone. In B. musculus it is 17 inches in length, the upper boundary formed by the palate plate of the maxillary for 13 of these, the 4 posterior by the frontal. The total *length of the nasal cavity*, measured straight from between the upper margins of the posterior and anterior nares, is in Megaptera 30 inches, in B. musculus 23, the shortness in the latter owing mainly to the more anterior position of the posterior nares on the basis cranii, partly to the nasal bones being 1½ inch shorter.

14. ETHMO-TURBINALS.—The lateral mass of the ethmoid bone is more developed in Megaptera, and there are two, if not three, turbinals; in B. musculus only one turbinal, with a rudiment of

a second. In Megaptera the lateral mass has a height of 3 to 4 inches, and projects inwards for 1 to 2 inches. The meatuses are—(1) Not seen in a front view, but felt by the finger at the back as a notch and short groove, directed horizontally forwards, rather above the level of the next. (2) Seen on the anterior third of the lateral mass, a groove 2 inches in length, large enough to receive the little finger but wedge-shaped: from below the middle of the mass, directed upwards and forwards, issuing and bifurcating at the anterior pointed end of the mass. Its inner edge is the turbinal, the free edge of the inner convex surface of the mass. (3) An inch below the hinder end of the latter begins the anterior end of the lower meatus, 1 to 1½ inch in width, ½ to ⅓ inch in depth, widening backwards for about 4 inches, where it is lost on the inferior surface of the mass. Its inner overhanging edge is the turbinal, narrow edged, a little curved, with the concavity to the meatus.

In *B. musculus* there is only the meatus which appears to correspond to the second of those above noted in Megaptera; but it is deeper and fissures the front of the mass so much that the meatus joins the narrow space of the roof. The meatus does not reach quite to the back. The turbinal is a narrow tongue of the lateral mass, with a deep groove between it and the roof of the cavity, which, in both B. musculus and Megaptera, is formed by a curved lamella reaching out from the mesethmoid. In B. musculus the lateral mass is not developed anteriorly and inferiorly, where No. 3 meatus occurs in Megaptera; but at the back the finger detects a notch and short wide groove, which may represent the back part of the 3rd meatus in Megaptera.

The *mesethmoid* also differs here. In Megaptera it comes down as a thick septum (1½ inch thick above, 3 inches below) nearly vertically for 2 inches and then slopes backwards, with about 1 inch deep excavation; in B. musculus, after a very short median projection, it becomes deeply excavated (3½ inches), the two laminæ 2 to 3 inches apart. The recess below this, which receives the lower part of the back of the mesethmoid cartilage, is, in B. musculus, about 4 inches deep, and large enough to receive the closed hand; in Megaptera it is about 1 inch deep.

15. Prenasal Space.—This wide gap, at and anterior to the blow-holes, is much wider in Megaptera, in which it is a narrow

ovoid, in B. musculus elliptical. The width posteriorly, in front of the nasals, is about 10 inches in both; greatest width, in Megaptera 14½ inches, in B. musculus 12½ inches; at the narrow anterior end, in Megaptera 4 inches, in B. musculus 3½. The widest part is, in Megaptera at 13 inches distal to the hollow end of the nasals, 11 inches distal to the temporal fossa, is at the middle of the first quarter of the beak, and just distal to the coronoid process of the premaxillary. In B. musculus the widest part is 17 to 18 inches distal to the hollow end of the nasals, and 6 inches along the beak from the temporal fossa. The widest part is, therefore, some way anterior to the distal end of the blow-holes, supposing these to begin near the hollow anterior border of the nasals. The distal end of the pre-nasal space is better marked off in B. musculus than in Megaptera; length of the space to this part, in Megaptera 30 to 31 inches, which carries it for a third of the way into the second quarter of the beak; length in B. musculus 25 inches, which carries it to about the middle of the first quarter of the beak. The limit is indicated by a rapid contraction to a low rounded angle. It is well to notice here that in these two skulls the width of the narrow inter-premaxillary space at the middle of the beak is, in Megaptera, 3 inches, in B. musculus 1¼.

The *vomer* here, the widest part of the space, is a little deeper in Megaptera, but differs considerably in width and form; contracting at the upper edge in B. musculus to 5¾ from 6⅝ some way below, while in Megaptera the upper edge is scarcely inverted, and the width is 7⅝ inches, in adaptation to the greater width of the prenasal space in Megaptera. The upper edge of the vomer also differs in thickness. In Megaptera it is thickest (1½ inch) at the back part of the prenasal space, and continues thus thick for some way within the nasal fossa; in B. musculus it is thickest (2¼ inches) at the middle of the prenasal space, and diminishes in thickness forwards and backwards.

16. Maxillary and Premaxillary Bones at the Nasal Region.—While in B. musculus the profile of these bones is here almost straight on to the beak, in Megaptera they present a marked fall from their posterior end for 7 or 8 inches along the beak, and from this hollow the *premaxillary* sends up a process which may be termed its *coronoid process.* Height of

process 1½ inch, base about 12 inches in length, beginning 2 inches anterior to the peak of the nasal bones; anterior slope of process the longest, summit from 5 to 6 inches anterior to the nasal peak. The height to which this process of the premaxillary rises in the hollow is just to the level of a straight line drawn from the top of the frontal process to the beak. The elevation of the surface of the head, referred to with the external characters, would appear to be a little anterior to this long elevation, as the blow-holes, 11 inches in length, were situated on the hinder slope of the elevation.

In Megaptera the parts of the premaxillary and maxillary at the side of the nasals and anterior to them, as they pass backwards are much inclined inwards, and bent with the convexity inwards, while in B. musculus they have very little inclination inwards. A line prolonged in the direction of the inner edge of the maxillary, from the beak, goes external to the frontal end of the frontal process—in Megaptera 5 inches, in B. musculus 1 inch. The contraction from the widest part of the prenasal space to between the frontal ends of the maxillaries is, in Megaptera from 14½ inches at the former place to 4 inches at the latter; in B. musculus from 12½ inches to 5. This, in Megaptera, is partly owing to the greater width of the prenasal space, partly to the greater inward encroachment of the temporal fossa at this part. Width between the frontal ends of the maxillaries, outer border, in Megaptera 11 inches, in B. musculus 14½. The frontal process of the maxillary is broader in Megaptera, and increases in breadth distally; at the top 3¼ inches, at 6 inches forwards 4 inches; and then sweeps broadly outwards in its distal half as the edge of the temporal fossa.

[In B. musculus the breadth of the frontal process of the maxillary at the top is 4 inches, at 12 inches forward only 2¼ inches, owing to the forward extension of the temporal fossa. The surface of the process is very convex transversely in Megaptera; in B. musculus it has very little transverse convexity.]

17. Ant-Orbital Process of the Maxillary.—The great length and backward and downward sweep of this process from the beak in Megaptera is characteristic. Length of process from beak 18 inches, with a fall of about 12 inches; in B musculus length about 15 inches, less as seen in front, with a

fall of about 6 inches. The form also is different, prismatic in Megaptera, flat in B. musculus. In B. musculus, where the process goes off, the curved border of the temporal fossa rises into a tubercle 2 inches high, 3 inches broad at the base. The border then twists forwards soon, overlapping the border from the beak, and forms the anterior edge of the flat process. This is the result of the forward extension of the temporal fossa in B. musculus. In Megaptera the prismatic form is owing to a lamina rising upwards and backwards, the edge of which is continued from the front edge of the temporal fossa. This lamina is represented in B. musculus by a low smooth ridge on the flat temporal fossa surface of the maxillary at 3 inches behind the anterior border of the process, while the tubercle in B. musculus is represented in Megaptera by a sharp even ridge running along the facial surface of the process. The outer end of the process in Megaptera is, in length externally, in front of the malar, 3 inches; in breadth, within the orbit, 6 inches; in B. musculus length 4½ inches, breadth within the orbit 6 inches.

The *overlapping of the frontal by the maxillary* is greater in Megaptera; breadth of the part overlapped 7 to 8 inches, bevelled marking on frontal 3 inches in length, but only 2 inches of it covered by the maxillary. In B. musculus breadth of angle overlapped 6 inches, the length overlapped 2 inches; no bevelled marking on frontal. Length of maxillary uncovered by frontal in temporal fossa, in Megaptera 1 inch, in B. musculus 4 inches. The ant-orbital process is in Megaptera 1 to 1½ inch behind the frontal process; in B. musculus 9 inches in front of it.

18. THE BEAK.—A survey of the beak from before at once shows the well-known greater breadth, with more convex edges, in Megaptera, contrasting with its long tapering form in B. musculus. The actual length in Megaptera is 85 inches, in B. musculus 96. It is convenient to divide the beak into quarters. At the base of the beak the breadth, along the curve, is less in Megaptera than in B. musculus (45 and 48 inches), and at the end of the first quarter (Megaptera 33½, B. musculus 36); but after this the breadth is greatest in Megaptera, at the middle Megaptera 27½, B. musculus 27; at the end of the third quarter, Megaptera 19½, B. musculus 17. The measurements given

in the table show to what extent these breadths belong to the maxillary, premaxillary, or to the mesial space. At the base, and at the end of the first quarter, the prenasal space and the direction of the surface of the premaxillary affect the measurements. At the middle of the beak the greater breadth in Megaptera is owing to the mesial space, which is nearly 2 inches wider than in B. musculus, but at the end of the third quarter nearly half of the decidedly greater breadth in Megaptera than in B. musculus is owing to the maxillary. Viewed from above, the breadth of the beak in Megaptera has very much the appearance of being less in front of the base than at the end of the first fourth, but the form deceives the eye; the narrowest part is behind the middle of the first quarter (33 inches), and from that part the breadth diminishes forwards.

The fall of the upper surface of the beak to its outer edge is on the posterior half, greatest in B. musculus, on the anterior half greatest in Megaptera. The amount of the fall at the base, at the end of the first quarter, at the middle, and at the end of the third quarter, respectively, is, in inches, in Megaptera 10, $4\frac{1}{2}$, $3\frac{3}{8}$, $2\frac{1}{2}$; in B. musculus $10\frac{1}{2}$, 5, 3, $1\frac{7}{8}$. This greater slope of the distal half of the beak in Megaptera is manifest to the eye. The surface is less convex transversely in B. musculus, giving the distal half of the beak a very flat appearance in B. musculus. In Megaptera the maxillary is convex transversely about the middle, with a slight concavity internal to this, but the chief transverse convexity is on the premaxillary, which is so great, on the second quarter and on part of the third quarter, that the highest part of the beak is on the surface, not at the inner border, as it is along the distal half of the beak. The line of articulation between the maxillary and premaxillary is, in Megaptera concave outwards on the two middle quarters (concavity $1\frac{1}{4}$ inch deep), convex outwards on the distal quarter. In B. musculus these undulations are much more gentle, the concavity of the first about $\frac{3}{4}$ inch deep.

Premaxillary Bone.—Besides the transverse convexity above noted, the premaxillary in Megaptera is later in undergoing the seeming twist of the surface. In B. musculus the premaxillary, very concave along the distal half of the prenasal space, becomes nearly horizontal at about a third of the distance

into the second quarter of the beak, and also nearly flat, except that there is a shallow groove along its inner third (prolonged from the concavity at the prenasal space) and a gentle convexity on the outer third.

In Megaptera the premaxillary on the distal half of the prenasal space is scarcely concave, and at the end of the first quarter of the beak the surface looks more inwards than upwards, and does not become horizontal till near the middle of the beak.

This seeming twist of the premaxillary, however, is not in reality a torsion of a flat bone, but is owing to the development of a transverse plate, beginning on the distal half of the prenasal space, which goes inwards and contracts that space. The premaxillary thus attains a sharply triangular form in transverse section. The internal or nasal surface is very concave in Megaptera from the end of the prenasal space onwards; in B. musculus the cavity does not begin till near the middle of the beak. In Megaptera the internal lamina is much more developed on the second quarter of the beak than onwards from this, the approximation of the premaxillaries being accomplished along the distal half by the more inward position and more inward slope of the vertical plate of the bone. In B. musculus the inward plate of the premaxillary appears to overhang to about the same extent throughout.

The *width of the inter-premaxillary space* along the distal three-fourths of the beak is, at the beginning of each quarter, respectively, in inches, in Megaptera, $8\frac{1}{2}$, 3, $2\frac{1}{2}$; in B. Musculus, $2\frac{1}{4}$, $1\frac{1}{8}$, $1\frac{3}{4}$. On the distal quarter, in Megaptera it continues to contract gradually to $1\frac{1}{4}$ inch at the point; in B. musculus it at first widens to 2 inches, and then contracts, width at the point about $\frac{3}{4}$ inch.

19. FORAMINA ON THE FACIAL SURFACE OF THE MAXILLARY. —These large foramina present differences in Megaptera and B. musculus, but reliance cannot be placed on characters which differ considerably on the two sides of the same skull. In Megaptera, however, they are larger, extend more into the second quarter of the beak, and are on the whole more internal in position than in B. musculus. In the latter they are 9 in number on each side, not symmetrically placed, and are on the

first quarter of the beak, 5 inches within the line, except one on the left side, which is on the second quarter 3 inches beyond the line. In Megaptera they are, on the right side, 7 large, 3 very small; on the left side, 10 large and one very small. Even at the base of the frontal process they are not symmetrical; right side, one large foramen (corresponding to the infra-orbital foramen in man), directed backwards and outwards, admitting two fingers; on left side, three foramina, each admitting a finger, the upper one with the reverted direction. The other foramina are too unsymmetrical to admit of individual comparison. On the left side two are on the line between the first and second quarters of the beak, and two are respectively 3 and 5 inches into the second quarter; on the right side one is on the line and one 3 inches beyond it on the second quarter. The most distal one is large on the left side, three times as large as on the right side. The foramina on the palatal aspect are more distinctive.

20. THE BEAK ON THE PALATAL ASPECT.—The chief differences here are the greater breadth of the median beam and the partial absence of the vascular grooves in Megaptera. The measurements given in the table show also that the depth of the hollow on each side of the median beam is much less on the posterior part of the beak in Megaptera. The narrow keel-like median beam in B. musculus gives it the appearance of greater projection, but the following measurements, taken at the junction of the first and second quarters of the beak, will show that the projection is less, and also the greater thickness of the beam in Megaptera. Median beam below level of outer edge of beak, in Megaptera 10½ inches, in B. musculus 8½; breadths of median beam, at two inches up, Megaptera 3¾ inches, B. musculus 3; at mid-height, 6 inches up on the slope, Megaptera 8 inches, B. musculus 6; at level of outer margin of beak (12 inches up, on the slope, in Megaptera, in B. musculus 8½ inches up), Megaptera 15 inches, B. musculus 8¼; concavity taken on level with outer margin of beak, in Megaptera, width 8 inches, depth 1; in B. musculus, width 12¾ inches, depth 2.

Seen in profile, the lower edge of the median beam of the palate is less curved in Megaptera; depth of concavity in [Mega]ptera 3 inches, along the maxillary part only, 2 inches;

depth in B. musculus 4 inches, along the maxillary part only, 2 inches.

The breadth of vomer exposed between the lower edges of the maxillaries is, in Megaptera about 1½ inch all along, except about the middle when it is increased to 2½ inches; behind, between the palatals, ½ inch in vomer is seen, increasing forwards. In B. musculus, along the anterior half, about ½ inch, on the posterior half, ¾ to 1 inch in breadth of the vomer is seen. The bony vomer extends to within 27 inches of the point of the beak in Megaptera, to within 15 inches in B. musculus.

21. Vascular Grooves on the Palatal Surface of the Maxillary Bone.—This system of great palatal grooves, and their foramina, will be better understood by observing them first in *B. musculus*. They are great grooves ⅜ to ½ inch broad, such as might be made with the end of the finger on a soft surface. They may be classified as (*a*) those of the roof, belonging to the whalebone region, and (*b*) those of the median beam. Those of the latter (*b*) issue from the fore-end of the palato-maxillary fissure, at least 3 in number, descend along the beam with more or less obliquity, one of the three arched up and covered for a time on the right side, on the left side two are thus arched and covered. The most anterior one reaches the lower edge of the beam at about the middle of the second quarter of the beak, and ceases at the middle of the beak. (*a*) Those of the whalebone region may be classified as anterior or longitudinal, seen on more than the anterior three-fourths of the beak; the intermediate, seen on the posterior half of the first quarter of the beak; and the posterior, seen below the temporal fossa. Of the *anterior or longitudinal series*, three issue on the anterior half of the first quarter of the beak, the external first, the third at the end of the first quarter, a fourth some way along the second quarter. The two last of these run along the inner part of the roof, where the roof meets the median beam, close together as great grooves, half an inch in breadth and deep enough to receive half the thickness of the finger, the one that is last to appear going on to the point of the maxillary, seen along a course of about 5 feet. The *intermediate series*, 3 in number, issue in the roof 9 to 8 inches from the outer edge, pass obliquely outwards and forwards for about 6 inches,

bifurcate and cease at about 3 to 4 inches from the outer edge, at the first quarter of the beak. The *posterior series*, 3 or 4 in number, issue in a line with the latter series, below the temporal fossa, back to near the hinder edge of the maxillary plate. They pass forwards and outwards, more curved than the intermediate series (concavity backwards), bifurcate, and may then curve partly backwards; but in B. musculus (in contrast with the posterior series in B. borealis) these sub-temporal grooves do not at first turn backwards, although at the very back, where the bone is much perforated and scaly, there may be a small exception to this. They, too, have a course of about 6 inches before they bifurcate and cease.

In *Megaptera* this grand system of grooves is deficient except the longitudinal series along the beak, and partly on the median beam, being in other parts replaced by foramina only with occasional short grooves. On the median beam two grooves are seen to begin at the fore-end of the palato-maxillary fissure, the lower one, the greatest and longest, 1 inch broad, passing downwards, and lost before the end of the first quarter of the beak is reached. Three longitudinal roof-grooves appear successively on the second quarter of the beak, and one runs on to the end. The intermediate roof-series are represented on the first quarter of the beak by apertures with very short grooves, one large aperture and two or three smaller, at distances of only 4, 5, and 6 inches from the outer edge of the beak. In the sub-temporal region, there are the foramina and scales of bones overhanging shallow spaces, but not a system of grooves like that of B. musculus. The cause of this deficiency of intermediate and posterior roof-grooves in Megaptera is the great breadth of its median beam, narrowing and filling up the concavity on each side, and more or less roofing over what are grooves in B. musculus. The position of the apertures of the intermediate and posterior series, it will have been noticed, is, accordingly, much farther out in Megaptera than in B. musculus.

22. Cranial Cavity.—The measurements given in the table show that the height is the same in both, that in Megaptera the breadth is greater by $\frac{1}{8}$ part (2 inches), the length less by 1 part (4 inches) than in B. musculus. This accords with the ortions of the back part of the skull externally, but the

whole cavity appears to be more capacious in B. musculus. The opening of the *olfactory fossa* is triangular in form, base below, and smaller in Megaptera; in B. musculus bluntly triangular, base above with a narrow notch at the middle (Megaptera, breadth 3 inches, height 2; B. musculus, breadth 3¼, height 3). The fossa itself in Megaptera is directed more upwards, is curved, and is shorter than in B. musculus (Megaptera 4 inches, B. musculus 5).

Other Characters within the Cranium.—In Megaptera the suture between the post and pre-sphenoid (10 inches from the foramen magnum) is open across its whole breadth; in B. musculus there is a short transverse ridge at the middle in the corresponding position (12 inches from foramen magnum), but no suture visible. Where the basi-occipital and post-sphenoid appear to have united, there is in Megaptera (5 inches from the foramen magnum) a curved ridge, as prominent nearly as a finger laid on flat, curved, convexity backwards; in front of it a wide shallow fossa; going back from it a similarly raised median ridge, on each side of which is a rounded fossa. In B. musculus the transverse ridge (8 inches from the foramen magnum) is very low, the median ridge behind is well marked but broad, and there is no fossa at the side of it. The sella turcica, about 3 inches long in both, is better marked in Megaptera, having a transverse depression on its anterior half; in B. musculus there is rather a transverse convexity, with a slight longitudinal median depression. The common orbital foramen, representing the optic foramen and sphenoidal fissure (which are separate in B. rostrata), is in Megaptera partly divided into optic and sphenoidal fissure parts by a well-marked peak of bone above and below, the intersphenoid suture intersecting the lower peak. If this partial subdivision did not exist in Megaptera, the common foramen would form a triangle wider below than the common foramen in B. musculus. In the roof of the cranial cavity there is a well-marked sharp median ridge in B. musculus, much less developed in Megaptera.

(*To be concluded in the April Number.*)

THE LIMITS OF HEARING. By J. Kerr Love, M.D.[1]

The paper deals with the Limits of Hearing under the following heads:—

1. The lowest audible notes.
2. The highest audible notes.
3. The perception of small differences in pitch.
4. The distance at which a note of given intensity can be heard.
5. Tone or note-deafness.

After noticing the attempts of Sauveur, Chladni, Biot, Wollaston, Savart, Despretz, and Helmholtz to determine the lower limits of hearing, the experiments of Professor Preyer of Jena having the same object in view, are given at some length. These experiments were made with very large tuning-forks, and with a series of vibrating metallic tongues. The conclusions drawn regarding this part of the subject are, that notes produced by fifteen or sixteen vibrations per second are the lowest which can be heard by the human ear. The difficulty of producing vibrations of sufficient amplitude to make such notes heard is great; but it is probable that sounds caused by a smaller number of vibrations are perceived as separate impulses, and not as true musical sounds. Many ears cannot hear notes caused by less than twenty-four vibrations.

In discussing the highest audible notes, the works of Sauveur, Chladni, Wollaston, and Despretz are again noticed, and the very important experiments of Dr Preyer with the series of forks made by Herr Appunn are given in detail. The convenient test afforded by Mr Galton's whistle is also noticed at length.

Dr Love describes small open pipes which he has made for testing the upper limits of hearing. These measure from 5 to 6 mm. long and 2 to 3 mm. in diameter, and give distinct notes of from 20,000 to 25,000 vibrations per second, calculated on the corrected plan necessary when dealing with such small pipes. The fact that diameter as well as length has to be noticed in dealing with these, and indeed with all pipes, is emphasised, and a simple experiment described showing this influence of diameter.

The bulk of the paper is given to the determination of the smallest appreciable difference in pitch. After describing Dr Preyer's work in this department of the subject, Dr Love thus describes his own instrument:—

"The instrument I use for testing appreciation of small differences

[1] Abstract of a Thesis presented to the University of Glasgow for the degree of M.D.

of pitch consists of closed organ pipes, which can be shortened or lengthened by movable stoppers. The stoppers are controlled by very carefully-adjusted screws, having a known number of turns to the inch. At the top of each screw is a horizontal index-plate, round which a pointer turns. The plate is graduated to twentieths of its circumference, and as the screw is moved by the turning of the handle of the revolving pointer, the pipe can be lengthened or shortened by an amount corresponding to any distance greater than that represented by a twentieth of a turn.

"The two screws I use have twenty-one and forty-two turns to the inch respectively. The stoppers can be made to advance or recede within the pipe through any distance from 3 inches—the entire length of the screws—to $\frac{1}{420}$ or $\frac{1}{840}$ of an inch, the value of a twentieth of turn for the screws respectively.

"Behind an upright, to which the screws and pipes are fastened, is the bellows which supplies the pipes with wind. This falls through a short distance (about 2 inches) under a weight of 3 or 4 lbs., producing a note from the pipes of from $1\frac{1}{2}$ to 2 seconds in duration. The fall of the bellows is checked by its contact with two horizontal bars placed at its ends. Unless thus checked, the tone begins to flatten very appreciably, when the supply of wind is almost exhausted. The note is brought to even a better and sharper termination if the bellows be caught up by the handle, the chief use of which is to raise the bellows preparatory to its fall. The bellows descends between anterior and posterior and lateral black-leaded slips, which prevent rocking. The same loudness, duration, quality, and steadiness of successive tones is thus ensured, for the sounds are produced by the same volume of air expelled under a constant pressure. The pipes I have used chiefly are the 1 foot 6 inches and 3 inches closed pipes, giving notes of 256, 512, 1024, and 2048 vibrations per second. The 3 inches pipe produces the two latter notes at its upper and lower ends respectively. Longer pipes than the largest of these make the instrument clumsy. The body of the pipes is made of brass, to allow of the fitting of air-tight stoppers, and of the application of a clamp to prevent the rising of the pipe under the application of the screw. A movement of the stopper through a given distance produces a different interval at different parts of the scale. For the coarser screw I found that eight turns produced an interval of a semitone at the 512 C; sixteen turns were required for the same interval at middle (256) C, and four and two turns for the two upper C's respectively. For the finer screw, of course, a similar interval required twice the number of turns; hence the necessity in stating the relative sensitiveness of two ears, or the results of several observations on the same ear, to give the pitch at which the experiment was tried, or at least to translate the reading of the screw into one of an absolute interval.

(Another reason for giving the absolute pitch, or at least for giving the pitch to the nearest tone or semitone, is that the ear is said to be sensitive in a very different degree at the various parts of the scale.)

Table showing Value of Screws in Fractions of a Semitone.

	1 turn.		½ turn.		¼ turn.		$\frac{1}{10}$ turn.	
	Fine Screw.	Coarse.	Fine.	Coarse.	Fine.	Coarse.	Fine.	Coarse.
	sem.	sem.	sem.	sem.	sem.	sem.	sem.	sem.
256, . .	$\frac{1}{32}$	$\frac{1}{16}$	$\frac{1}{64}$	$\frac{1}{32}$	$\frac{1}{128}$	$\frac{1}{64}$	$\frac{1}{320}$	$\frac{1}{160}$
512, . .	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{32}$	$\frac{1}{16}$	$\frac{1}{64}$	$\frac{1}{32}$	$\frac{1}{160}$	$\frac{1}{80}$
1024, . .	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{32}$	$\frac{1}{16}$	$\frac{1}{80}$	$\frac{1}{40}$
2048, . .	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{40}$	$\frac{1}{20}$

"In using this instrument in the testing of the hearing of considerable companies I wrote out a list of fifteen to thirty-five tests, to which the observers were asked to listen. Each test was applied as follows:—A note in the neighbourhood of one of the C's was sounded and repeated, after which the screw was altered. As rapidly as possible the changed note was sounded, and the observer asked to put down his opinion of the third note in the words flat, sharp, or unchanged. Observers were seated as far apart as practicable, the working of the screws was hidden by a screen placed before them, and every precaution adopted to fix the attention of the observers on the experiment. They were asked never to guess, but on the other hand to give their ears the benefit of the slightest impression formed just after the sounding of the third or altered note."

Results got by this method should be taken as correctly representing the capacity of any class of observers, and not of its individual members. Trained musicians, *e.g.*, violinists, tuners, pianists, &c., were tested either singly or in very small companies, and every facility afforded of independent and deliberate judgment. In all about two hundred observers were tested, consisting of miscellaneous non-musical companies, church choirs, pianists, and violinists. The results are briefly as follows:—

The least observable difference of pitch is for untrained and slightly trained ears difficult to state, but (exclusive of cases of tone-deafness) may be put down as from $\frac{1}{8}$ to $\frac{1}{40}$ semitone. A twenty-fourth semitone is a common limit. The ears of such trained musicians as violinists, tuners, and some pianists can detect with certainty a difference of $\frac{1}{64}$ to $\frac{1}{80}$ semitone. All observers, but especially the untrained, detect sharpened better than flattened intervals. Generally speaking, Weber's Law holds good for all but the highest and lowest parts of the musical scale. A remarkable case, that of a gentleman whose ear is keen for the appreciation of small intervals, but who is deaf to all notes above D^{v} (475·2 vibrations), is given. He hears C^{v} (4220) distinctly on the organ, but hears nothing when E^{v} (5280) is sounded.

Dr Love considers that no quite satisfactory test has yet been found for the distance at which a sound of given intensity can be

heard. He thinks Politzer's acoumeter the best and most convenient test we have, and that it can be heard by normal ears in almost perfect stillness at a distance of 15 or 16 metres.

Tone or note-deafness is discussed and some instances given, and the conclusion drawn that such cases of deafness (deafness to intervals of a whole tone or more) are very rare, but that some well-authenticated instances have been recorded.

ABNORMAL ARRANGEMENT OF THE KIDNEY AND ITS VESSELS. By R. Bodkin Mahon, M.D., M.Ch.

The following state of affairs was noticed in connection with the right kidney in the abdomen of a female subject undergoing dissection during last session in the anatomical room of Queen's College, Cork. The viscus lay in the right iliac fossa, its lower end lying over the right common iliac artery. The size of the kidney was less than normal—a deficiency which was compensated by a marked increase in size of the left kidney. The misplaced kidney possessed nothing of the characteristic reniform shape, resembling more a flattened oval.

The ureter arose from a depression on the anterior surface, by four branches which, soon uniting, formed a single tube descending on the anterior surface of the kidney.

Five arteries entered the organ, and were thus arranged:—

1. A large branch arose from the side of the aorta at the usual point of origin of the renal arteries. This artery descended behind the vena cava, and entered the kidney at the junction of the upper and middle two-thirds of its inner border.
2. This branch, smaller than the preceding, but larger than any of those succeeding, arose 1½ inch above the bifurcation of the aorta. It entered the kidney at its inner border, and with all the remaining branches, passed in front of the inferior vena cava.
3. A branch arose ¼ inch below No. 2 from the side of the aorta. It divided into two branches of equal size before entering the gland. These branches entered the kidney at the depression on its anterior surface, corresponding to the hilus.
4. This branch arose from the front of the bifurcation of the aorta. It entered the kidney at the lower third of its inner border.
5. The last branch arose from the outer side of the commencement of the right common iliac artery. It passed behind the kidney, and entered its substance by piercing the convex outer border.

The renal veins entering the cava numbered three:—

1. A small vein accompanying arterial branch No. 3.
2. A very small vein attending arterial branch No. 5.
3. What may be called the renal vein proper arose by three branches from the front surface of the kidney. They lay in a plane posterior to the ureter, but anterior to the arteries. The two branches arising lowest down quickly united to form a single trunk, which was joined by the ovarian vein of the

right side. It passed upwards and outwards to the upper end of the kidney. Here, turning inwards, it was joined by the remaining branch. The resulting trunk formed a large vein, which entered the vena cava a little lower down than the vein of the opposite side.

Both renal and ovarian veins were large, and distended with blood.

The suprarenal body was found attached by fibrous tissue to the under surface of the back part of the right lobe of the liver. Its shape was hemispheroidal. It had no connection with the kidney.

The most interesting points about the case are, the branch from the bifurcation of the aorta, the fact of only one branch entering the kidney at what may be considered the hilus, and the condition of the renal and ovarian veins.

In Quain's work on the arteries, pl. lvii. fig. 3 shows a condition somewhat similar to the above case. Here, however, all the arteries enter the hilus of the gland. In reported cases of abnormal arrangement of the kidney and its vessels, the condition of the renal veins has apparently escaped observation, at least I can find no record of a similar condition existing to that I have described above.

It may not be uninteresting to add, that in the same subject each common carotid bifurcated at the level of the cricoid cartilage. There was also a large thyroidea ima from the innominate.

ACCESSORY PHRENIC NERVE. By F. Charles Larkin, M.R.C.S., &c., *Demonstrator of Physiology, University College, Liverpool.*

This variation was observed in the dissection of the body of a male adult on April 14, 1888.

On each side there was an ordinary phrenic nerve, which arose from the 3rd and 4th cervical nerves, and had a communicating branch from the 5th. Its course through the chest was quite usual.

Each accessory phrenic, which was ¼ to ⅛ the size of the normal nerve, arose from the 5th cervical nerve. It crossed the anterior scalenus parallel to, but ¼ inch external to, the ordinary nerve.

In the chest, between the pericardium and the pleura, the right accessory nerve was 1 inch to 1½ inch in front of normal nerve, while the left accessory was ¼ to ½ inch behind its companion.

In each case the accessory nerve joined the phrenic just before it divided into its terminal branches.

The accessory phrenic gave several branches to the pleura and pericardium, while the true nerve seemed to give none.

Note.—Specimens of accessory phrenic nerve have also been described by Professor Turner in this *Journal*, November 1871 and May 1874, and by Professor D. J. Cunningham in November 1872.

Journ. of Anat. & Phys. Jan.y 1889.

Vol. XXIII / N.S. Vol. III } Pl. VII.

Fig. 1.

Fig. 2.

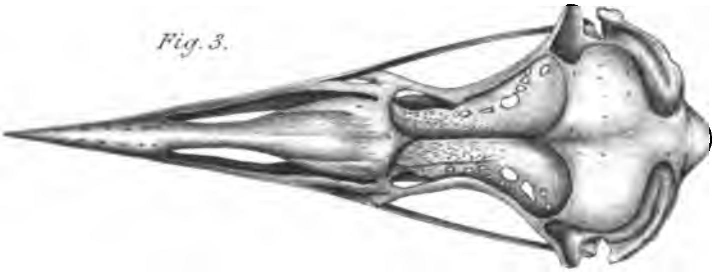

Fig. 3.

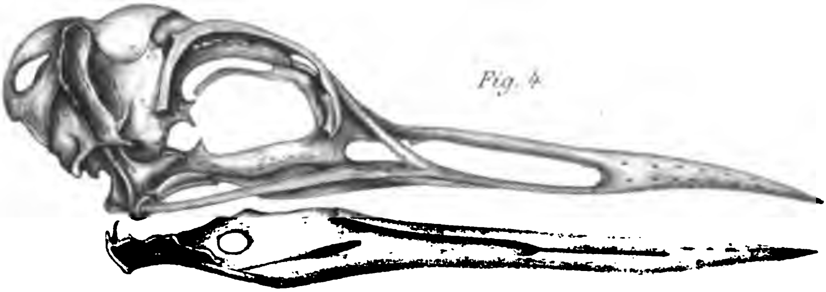

Fig. 4.

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ARCTIC & SUB-ARCTIC WATER BIRDS.

Fig. 5.

Fig. 6.

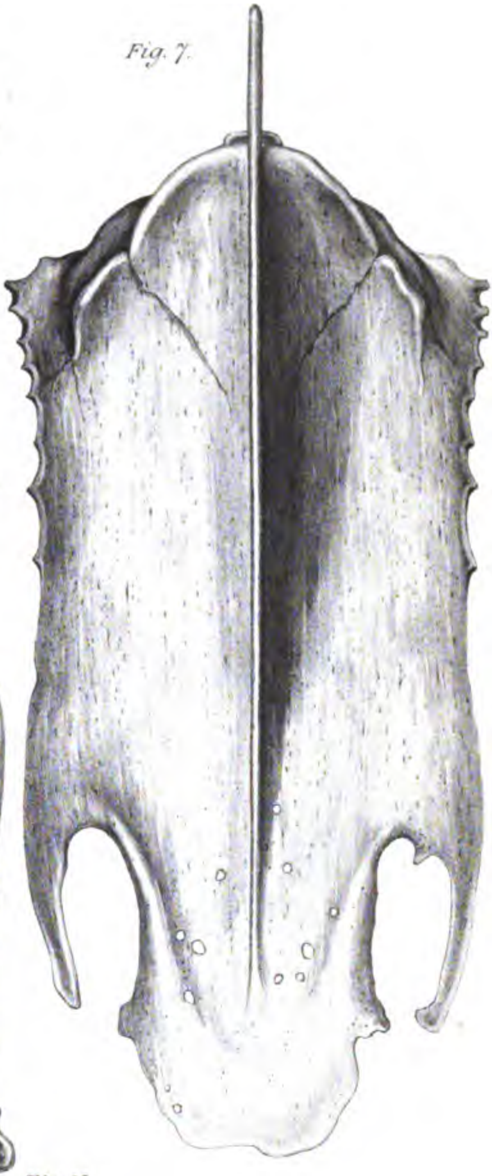

Fig. 7.

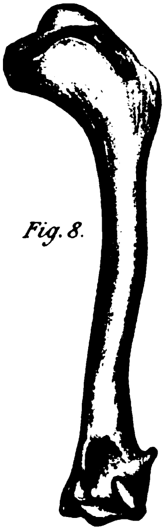

Fig. 8.

Fig. 9.

Fig. 10.

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ARCTIC & SUB-ARCTIC WATER BIRDS.

Journ. of Anat. & Phys., Jan.y 1889.

Vol. XXIII / N.S. Vol. III } Pl. IX.

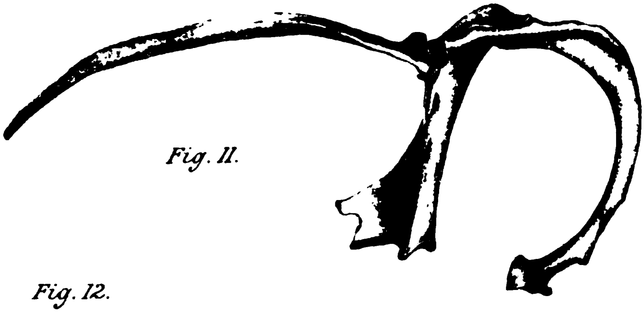

Fig. 11.

Fig. 12.

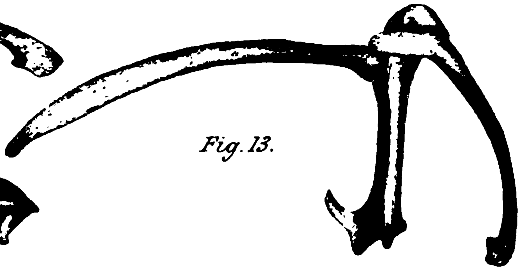

Fig. 13.

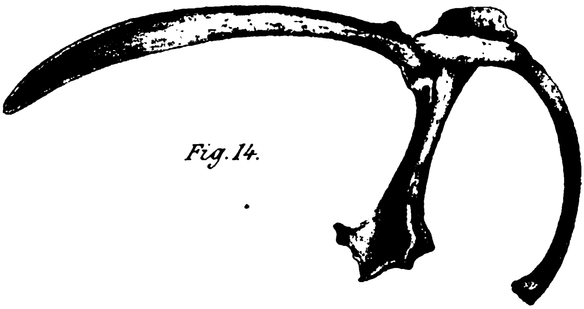

Fig. 14.

Fig. 15.

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ARCTIC & SUB-ARCTIC WATER BIRDS.

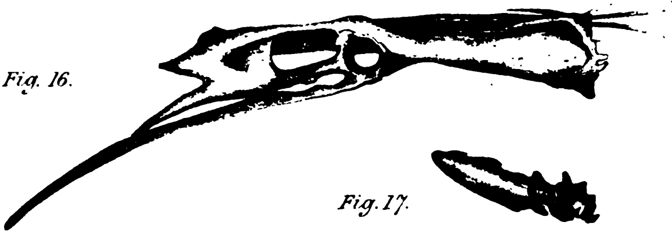

Fig. 16.

Fig. 17.

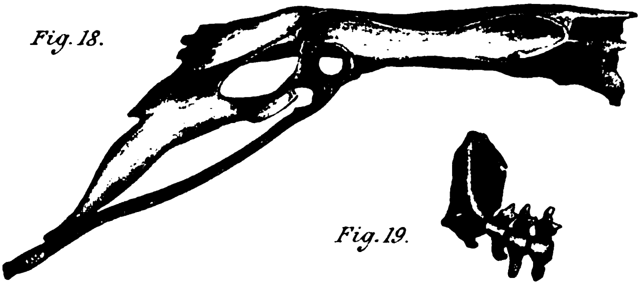

Fig. 18.

Fig. 19.

Fig. 20.

Fig. 21.

Fig. 22.

R.W. Shufeldt del. F Huth, Lith^r Edin^r

ARCTIC & SUB-ARCTIC WATER BIRDS.

Journ. of Anat. & Phys. Jan.[y] 1889.

Vol. XXIII / N.S. Vol. III } Pl. XI.

Fig. 23.

Fig. 24.

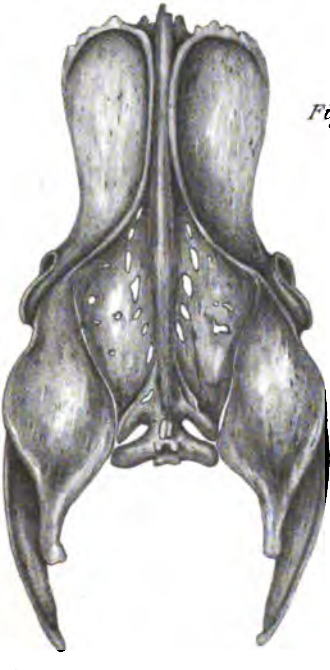

Fig. 25.

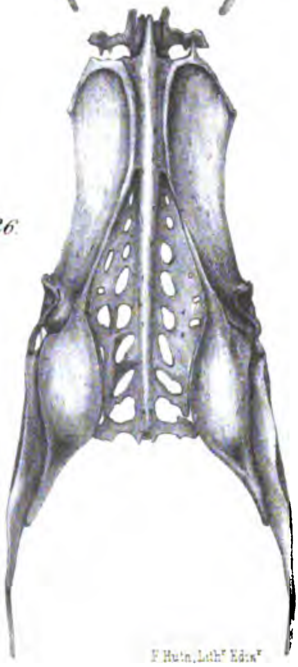

Fig. 26.

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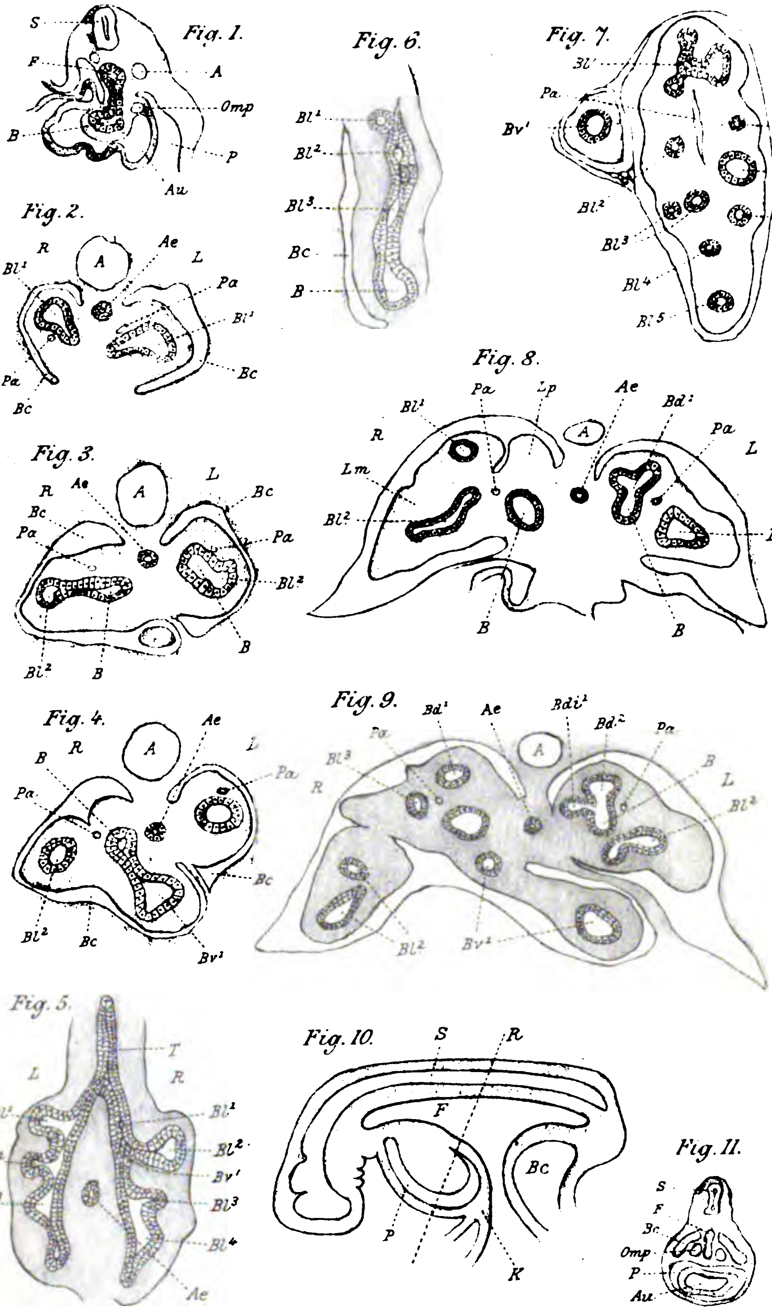
ARCTIC & SUB-ARCTIC WATER BIRDS.

Journ. of Anat. & Phys., Jan^y 1889.

Vol. XXIII / N. S. Vol. III } *Pl. XII.*



F. Huth Lith^r Edin^r

DEVELOPMENT OF LUNGS.

Journal of Anatomy and Physiology.

THE RELATIONS BETWEEN THE SUPERFICIAL ORIGINS OF THE SPINAL NERVES FROM THE SPINAL CORD AND THE SPINOUS PROCESSES OF THE VERTEBRÆ.[1] By R. W. Reid, F.R.C.S., *Lecturer on Anatomy in the Medical School of St Thomas's Hospital.* (Plates XIII., XIV.)

Owing to the somewhat insufficient data afforded regarding the exact position in the adult of the superficial origin of the spinal nerves from the spinal cord in relation to the surface of the body, I have been led to make a series of dissections to try to localise, if possible, these positions, partly to obtain data of a purely anatomical character, and partly because the subject is one which interests, and is likely still further to interest, physicians and surgeons in diagnosing and treating certain diseases of the spinal cord or its membranes.

On account of the very deep position of the spinal cord, and considering that its investing column is so covered by muscle posteriorly, the only surface landmarks which can be made use of are the posterior extremities of the spinous processes of the vertebræ. In most subjects these can be felt from the seventh cervical (it may be the sixth) to the first sacral by firmly pressing the point of the finger along the middle line of the back, especially if the spine be somewhat flexed.

Although the length and obliquity of the spinous processes vary a good deal, chiefly in the dorsal region, yet I think their posterior ends may fairly be made use of for the purpose.

Before describing the methods I adopted to obtain the rela-

[1] Read before the Anatomical Society of Great Britain and Ireland, November 1888.

tions and the result of the investigation, I may say that, from an examination of a number of spinal cords, I find that practically the posterior roots and the anterior roots of nerves belonging to the same segment leave the cord at the same level. The maximum variation, either with regard to the vertical area of the superficial origin of the anterior roots as compared with one another, of the posterior roots as compared with one another, or of the anterior and posterior roots of nerves of the same segment as compared with one another, was 3 mm. This variation occurred in the difference of height of the area of origin of the anterior root as compared with that of the posterior root in a nerve in the lower dorsal region.

The plan I adopted is as follows:—After clearing away the muscles of the back and cleaning the spinal processes, posterior surfaces of the laminæ, articular processes, transverse processes, and adjoining ribs as far as their angles (leaving the ligaments undisturbed), I removed one half of each neural arch by sawing down the middle of each spinous process and cutting the laminæ of one side close to the articular processes. I then opened the dura mater in the middle line behind and turned it to one side, and by carefully removing the arachnoid I obtained a view of the posterior roots of the spinal nerves from their emergence from the cord to their entrance into the inner surface of the dura mater. I thus left intact one half of the spinous processes, the supra spinous ligament, part of the ligamentum nuchæ and the interspinous ligaments, and so preserved as nearly as possible the natural curvatures of the spinal column. The exact limits of the superficial origin of the nerve roots were marked by running fine pins into the substance of the cord.

In order to obtain an orthographic projection such as the one I present to you (Pl. XIII.), the method I adopted, with the kind assistance of Mr Shattock, was as follows:—The specimen being laid in the horizontal position with its anterior surface downwards, a sheet of glass was placed horizontally over it. I then traced upon the glass the vertical projection of the outline of the bones, cord, and nerves by using a prismatic block of wood whose axis was vertical to the glass. By directing the eye along one edge of the prism to any point of

the specimen, we traced the outline of the specimen upon the glass. I then transferred this outline to a sheet of paper, and tested its accuracy by carefully comparing with a pair of dividers all parts of the outline with corresponding parts of the specimen. Then by using a pantograph I reduced the drawing one half, and thus obtained an outline exactly one half the natural size (Pl. XIII.).

The mode I adopted in order to get the relations between the vertical areæ of the superficial origins of the posterior roots of the spinal nerves and the posterior extremities of the spinous processes when the body is erect is as follows:—The specimen was hung vertically from a horizontal bar, placed antero-posteriorly, by means of a cord fixed in the skull in a vertical line through the middle of each condyle of the occipital bone. A sheet of paper was suspended from the bar, and the upper and lower limits of the posterior ends of the spinous processes and the upper and lower limits of the posterior roots of the spinal nerves, as they emerged from the cord, were ruled off upon the paper by holding one edge of a set square horizontally, one of the acute angles of square touching these limits. The ruling edge of the square was kept horizontal by holding the square in such a way that a plumb-line suspended from the horizontal bar corresponded with one of a series of lines drawn upon the square at right angles to the horizontal edge before mentioned.

The result of this investigation, carried out upon six specimens, is shown in the following table, where A = the upper limit and B = equal the lower limit of the superficial origin of a spinal nerve from the spinal cord. All the specimens were taken from adult male subjects with the exception of No. 5, which was an adult female one. No. 3 presented an extra lumbar vertebra.

TABLE.

Nerves.	Specimen. No.		
2nd Cervical.	1.	A.	Upper border of posterior arch of atlas.
		B.	Lower border of posterior arch of atlas.
	2.	A.	Just above lower border of posterior arch of atlas.
		B.	Midway between posterior arch of atlas and spine of axis.
	3.	A.	Upper border of posterior arch of atlas.
		B.	Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of posterior arch of atlas.

Nerves.	Specimen. No.	
2nd Cervical	4.	A. A little above the upper border of the posterior arch of atlas.
		B. Lower border of posterior arch of atlas.
	5.	A. Middle of posterior arch of atlas.
		B. Junction of upper $\frac{1}{3}$ and upper $\frac{2}{3}$ of interval between posterior arch of atlas and spine of axis.
	6.	A. Lower border of posterior arch of atlas.
		B. Little below middle of interval between posterior arch of atlas and spine of axis.
3rd Cervical.	1.	A. Just below the lower border of posterior arch of atlas.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of axis.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between posterior arch of atlas and spine of axis.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of axis.
	3.	A. Middle of interval between posterior arch of atlas and spine of axis.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of axis.
	4.	A. Just below lower border of posterior arch of atlas.
		B. Just above upper border of spine of axis.
	5.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between posterior arch of atlas and spine of axis.
		B. Middle of spine of axis.
	6.	A. Upper border of spine of axis.
		B. A little below middle of spine of axis.
4th Cervical.	1.	A. A little below middle of spine of axis.
		B. Just above the lower border of spine of axis.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 3 c.
		B. Just above the upper border of spine of 3 c.
	3.	A. Just below lower border of spine of axis.
		B. Upper border of spine of 3 c.
	4.	A. Just below upper border of spine of axis.
		B. Just below lower border of spine of axis.
	5.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of axis.
		B. Middle of intervals between spines of 2 c. and 3 c.
	6.	A. A little below middle of spine of axis.
		B. Middle of spine of 3 c.
5th Cervical.	1.	A. A little above the lower border of spine of 3 c.
		B. A little above the spine of 4 c.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 2 c. and 3 c.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 3 c. and 4 c.
	3.	A. Lower border of spine of 3 c. to just above lower border of spine of 4 c.
		B. Just above lower border of spine of 4 c.
	4.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 2 c. and 3 c.
		B. Lower border of spine of 3 c.
	5.	A. Upper border of spine of 3 c.
		B. Lower border of spine of 3 c.
	6.	A. Just below lower border of spine of 3 c.

Nerves.	Specimen. No.	
5th Cervical.	6.	B. Junction of upper ¼ and lower ¾ of interval between spines of 4 c. and 5 c.
6th Cervical.	1.	A. Junction of upper ¼ and lower ¾ of interval between spines of 4 c. and 5 c.
		B. Lower border of spine of 5 c.
	2.	A. Junction of upper ⅔ and lower ⅓ of interval between spines of 3 c. and 4 c.
		B. Junction of upper ⅔ and lower ⅓ of interval between spines of 4 c. and 5 c.
	3.	A. Lower border of spine of 4 c.
		B. Junction between upper ⅓ and lower ⅔ of spine of 5 c.
	4.	A. Just above lower border of spine of 3 c.
	4.	B. Lower border of spine of 3 c.
	5.	A. Lower border of spine of 3 c.
		B. Upper border of spine of 4 c.
	6.	A. Middle of interval between spines of 4 c. and 5 c.
		B. Just below lower border of spine of 5 c.
7th Cervical.	1.	A. Lower border of spine of 5 c.
		B. Just below upper border of spine of 6 c.
	2.	A. Junction of upper ⅔ and lower ⅓ of interval between spines of 4 c. and 5 c.
		B. Junction of upper ⅓ and lower ⅔ of interval between spines of 5 c. and 6 c.
	3.	A. Junction of upper ⅓ and lower ⅔ of spine of 5 c.
		B. Just above upper border of spine of 6 c.
	4.	A. Lower border of spine of 4 c.
		B. Junction of upper ⅓ and lower ⅔ of spine of 5 c.
	5.	A. Junction of upper ⅓ and lower ⅔ of spine of 4 c.
		B. Just below upper border of spine of 5 c.
	6.	A. Junction of upper ¼ and lower ¾ of interval between spines of 5 c. and 6 c.
		B. Junction of upper ¾ and lower ¼ of spine of 6 c.
8th Cervical.	1.	A. Just below upper border of spine of 6 c.
		B. Junction of upper ⅔ and lower ⅓ of interval between spines of 6 c. and 7 c.
	2.	A. Junction of upper ⅓ and lower ⅔ of interval between spines of 5 c. and 6 c.
		B. Just below middle of spine of 6 c.
	3.	A. Just above upper border of spine of 6 c.
		B. Middle of interval between spines of 6 c. and 7 c.
	4.	A. Junction of upper ⅓ and lower ⅔ of spine of 5 c.
		B. Junction of upper ⅔ and lower ⅓ of interval between spines of 5 c. and 6 c.
	5.	A. Just below upper border of spine of 5 c.
		B. Little above middle of interval between spines of 5 c. and 6 c.
	6.	A. Junction of upper ¾ and lower ¼ of spine of 6 c.
		B. Upper border of spine of 7 c.
1st Dorsal.	1.	A. Junction of upper ⅔ and lower ⅓ of interval between spines of 6 c. and 7 c.
		B. Junction of upper ⅓ and lower ⅔ of interval between spines of 7 c. and 1 d.

Nerves.	Specimen. No.	
1st Dorsal.	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 6 c.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 6 c. and 7 c.
	3.	A. Middle of interval between spines of 6 c. and 7 c.
		B. Middle of spine of 7 c.
	4.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 5 c. and 6 c.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 6 c. and 7 c.
	5.	A. A little above middle of interval between spines of 5 c. and 6 c.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of interval between spines of 6 c. and 7 c.
	6.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 7 c.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of interval between spines of 7 c. and 1 d.
2nd Dorsal.	1.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 7 c. and 1 d.
		B. Just below upper border of spine of 1 d.
	2.	A. Junction of upper $\frac{2}{3}$ with lower $\frac{1}{3}$ of interval between spines of 6 c. and 7 c.
		B. Just below lower border of spine of 7 c.
	3.	A. Middle of spine of 7 c.
		B. Junction of upper $\frac{3}{4}$ with lower $\frac{1}{4}$ of interval between spines of 7 c. and 1 d.
	4.	A. Middle of interval between spines of 6 c. and 7 c.
		B. Middle of spine of 7 c.
	5.	A. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of interval between spines of 6 c. and 7 c.
		B. Just below upper border of spine of 7 c.
	6.	A. Just below upper border of spine of 1 d.
		B. Just above lower border of spine of 1 d.
3rd Dorsal.	1.	A. Just above lower border of spine of 1 d.
		B. Middle of interval between spines of 1 d. and 2 d.
	2.	A. Middle of interval between spines of 7 c. and 1 d.
		B. Just below middle of spine of 1 d.
	3.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 1 d.
		B. Middle of interval between spines of 1 d. and 2 d.
	4.	A. Just above lower border of spine of 7 c.
		B. Upper border of spine of 1 d.
	5.	A. Middle of spine of 7 c.
		B. Middle of interval between spines of 7 c. and 1 d.
	6.	A. Just below lower border of spine of 1 d.
		B. Lower border of spine of 2 d.
4th Dorsal.	1.	A. Middle of interval between spines of 1 d. and 2 d.
		B. Middle of interval between spines of 2 d. and 3 d.
	2.	A. Just below lower border of spine of 1 d.
		B. Just above middle of spine of 2 d.
	3.	A. Middle of interval between spines of 1 d. and 2 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 2 d.
	4.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 1 d.
		B. Middle of interval between spines of 1 d and 2 d.

Nerves.	Specimen. No.	
4th Dorsal.	5.	A. Just below upper border of 1 d.
		B. Middle of interval between spines of 1 d and 2 d.
	6.	A. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of interval between spines of 2 c and 3 d.
		B. Just above middle of spine of 3 d.
5th Dorsal.	1.	A. Middle of interval between spines of 2 d. and 3 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 3 d. and 4 d.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 2 d.
		B. Just above upper border of spine of 3 d.
	3.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 2 d.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 3 d.
	4.	A. Middle of spine of 2 d.
		B. Middle of interval between spines of 2 d. and 3 d.
	5.	A. Upper border of spine of 2 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 2 d.
	6.	A. Just below middle of spine of 3 d.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 4 d.
6th Dorsal.	1.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 3 d. and 4 d.
		B. Just above lower border of spine of 4 d.
	2.	A. Little above middle of spine of 3 d.
		B. Just above middle of spine of 4 d.
	3.	A. Just below middle of spine of 3 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 3 d. and 4 d.
	4.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 3 d.
		B. Just below upper border of spine of 4 d.
	5.	A. Lower border of spine of 2 d.
		B. Middle of interval between spines of 3 d. and 4 d.
	6.	A. Just above middle of spine of 4 d.
		B. Just below upper border of spine of 5 d.
7th Dorsal.	1.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between 4 d. and 5 d.
		B. Junction of upper $\frac{4}{5}$ and lower $\frac{1}{5}$ of spine of 5 d.
	2.	A. Just below middle of spine of 4 d.
		B. Upper border of spine of 5 d.
	3.	A. Just above middle of spine of 4 d.
		B. Middle of interval between spines of 4 d. and 5 d.
	4.	A. Middle of spine of 4 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between 4 d. and 5 d.
	5.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 4 d.
		B. A little above middle of interval between spines of 4 d. and 5 d.
	6.	A. Junction of upper $\frac{1}{5}$ and lower $\frac{4}{5}$ of spine of 5 d.
		B. Junction of lower $\frac{1}{6}$ and upper $\frac{5}{6}$ of spine of 5 d.
8th Dorsal.	1.	A. Lower border of spine of 5 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 5 d. and 6 d.
	2.	A. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 5 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 5 d. and 6 d.

Nerves.	Specimen. No.	
8th Dorsal.	3.	A. A little below upper border of spine of 5 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 5 d. and 6 d.
	4.	A. Just above upper border of spine of 5 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 5 d. and 6 d.
	5.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of interval between spines of 4 d. and 5 d.
		B. Just below lower border of spine of 5 d.
	6.	A. Lower border of spine of 5 d.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 6 d.
9th Dorsal.	1.	A. Upper border of spine of 6 d.
		B. A little below middle of interval between spines of 6 d. and 7 d.
	2.	A. Junction of upper $\frac{4}{5}$ and lower $\frac{1}{5}$ of interval between spines of 5 d. and 6 d.
		B. A little above middle of interval between spines of 6 d. and 7 d.
	3.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 6 d.
		B. Just above upper border of spine of 7 d.
	4.	A. Just below middle of interval between spines of 5 d. and 6 d.
		B. Just above lower border of spine of 6 d.
	5.	A. Just above upper border of spine of 6 d.
		B. A little below middle of interval between spines of 6 d. and 7 d.
	6.	A. A little above middle of spine of 6 d.
		B. Lower border of spine of 6 d.
10th Dorsal.	1.	A. Just below upper border of spine of 7 d.
		B. Middle of interval between spines of 7 d. and 8 d.
	2.	A. A little below middle of interval between spines of 6 d. and 7 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 7 d.
	3.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 7 d.
		B. A little below middle of interval between spines of 7 d. and 8 d.
	4.	A. Middle of interval between spines of 6 d. and 7 d.
		B. Middle of spine of 7 d.
	5.	A. Upper border of spine of 7 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 7 d. and 8 d.
	6.	A. Middle of spine of 7 d.
		B. A little above middle of spine of 8 d.
11th Dorsal.	1.	A. Just above upper border of spine of 8 d.
		B. Lower border of spine of 8 d.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 7 d.
		B. Just above upper border of spine of 8 d.
	3.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 8 d.
		B. Just below lower border of spine of 8 d.
	4.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 7 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 8 d.
	5.	A. A little above upper border of spine of 8 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 8 d.

Nerves.	Specimen No.	
11th Dorsal.	6.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 8 d.
		B. Junction of upper $\frac{1}{6}$ and lower $\frac{5}{6}$ of spine of 9 d.
12th Dorsal.	1.	A. Just above middle of interval between spines of 8 d. and 9 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 9 d.
	2.	A. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 8 d.
		B. Lower border of spine of 8 d.
	3.	A. Middle of interval between spines of 8 d. and 9 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 9 d.
	4.	A. Lower border of spine of 8 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 9 d.
	5.	A. Middle of interval between spines of 8 d. and 9 d.
		B. Middle of spine of 9 d.
	6.	A. Middle of spine of 9 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 9 d. and 10 d.
1st Lumbar.	1.	A. A little above middle of interval between spines of 9 d. and 10 d.
		B. Lower border of spine of 10 d.
	2.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 8 d. and 9 d.
		B. A little below spine of 9 d.
	3.	A. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of interval between spines of 9 d. and 10 d.
		B. Just below upper border of spine of 10 d.
	4.	A. Just above lower border of spine of 9 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 10 d.
	5.	A. Lower border of spine of 9 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 10 d.
	6.	A. Junction of upper $\frac{1}{6}$ and lower $\frac{5}{6}$ of spine of 10 d.
		B. Lower border of spine of 10 d.
2nd Lumbar.	1.	A. A little below spine of 10 d.
		B. Just below upper border of spine of 11 d.
	2.	A. A little below middle of spine of 9 d.
		B. Middle of spine of 10 d.
	3.	A. Middle of spine of 10 d.
		B. Just above spine of 11 d.
	4.	A. Just above lower border of spine of 10 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 11 d.
	5.	A. Lower border of spine of 10 d.
		B. Upper border of spine of 11 d.
	6.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 10 d. and 11 d.
		B. Just above middle of spine of 11 d.
3rd Lumbar.	1.	A. Just below upper border of spine of 11 d.
		B. Just above lower of spine of 11 d.
	2.	A. Middle of spine of 10 d.
		B. Just above middle of interval between spines of 10 d. and 11 d.
	3.	A. Just above upper border of spine of 11 d.
		B. Middle of spine of 11 d.

Nerves.	Specimen No.	
3rd Lumbar.	4.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 11 d.
		B. Junction of upper $\frac{5}{6}$ and lower $\frac{1}{6}$ of spine of 11 d.
	5.	A. Middle of spine of 11 d.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of interval between spines of 11 d. and 12 d.
	6.	A. Middle of spine of 11 d.
		B. Just above lower border of spine of 11 d.
4th Lumbar.	1.	A. Just above lower border of spine of 11 d.
		B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 11 d. and 12 d.
	2.	A. Just above middle of interval between spines of 10 d. and 11 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 11 d.
	3.	A. Middle of spine of 11 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 11 d.
	4.	A. Just above lower border of spine of 11 d.
		B. Just below middle of interval between spines of 11 d. and 12 d.
	5.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of interval between spines of 11 d. and 12 d.
		B. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of interval between spines of 11 d. and 11 d.
	6.	A. Just below lower border of spine of 11 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 12 d.
5th Lumbar.	1.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of interval between spines of 10 d. and 11 d.
		B. Just below upper border of spine of 12 d.
	2.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 11 d.
		B. Just above lower border of 11 d.
	3.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of spine of 11 d.
		B. Just below upper border of spine of 12 d.
	4.	A. Just below middle of interval between spines of 11 d. and 12 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 12 d.
	5.	A. Junction of upper $\frac{3}{4}$ and lower $\frac{1}{4}$ of interval between spines of 11 d. and 12 d.
		B. Just below upper border of 12 d.
	6.	A. Junction of upper $\frac{3}{7}$ and lower $\frac{4}{7}$ of spine of 12 d.
		B. Junction of lower $\frac{2}{3}$ and upper $\frac{1}{3}$ of spine of 12 d.
6th Lumbar.	3.	A. Just below upper border of spine of 12 d.
		B. Just above lower border of spine of 12 d.
1st Sacral.	1.	A. Just below upper border of spine of 12 d.
	2.	A. Just above lower border of spine of 12 d.
	3.	A. Just above lower border of spine of 12 d.
	4.	A. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 12 d.
	5.	A. Just below upper border of spine of 12 d.
	6.	A. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of 12 d.
5th Sacral.	1.	B. Junction of upper $\frac{1}{7}$ and lower $\frac{6}{7}$ of spine of 1 l.
	2.	B. Lower border of spine of 12 d.
	3.	B. Middle of spine of 1 l.
	4.	B. Junction of upper $\frac{1}{8}$ and lower $\frac{7}{8}$ of spine of 1 l.

Nerves.	Specimen. No.	
5th Sacral.	5.	B. Just below lower border of spine of 1 l.
	6.	B. Just below lower border of spine of 1 l.
Coccygeal.	1.	A. Junction of upper $\frac{1}{7}$ and lower $\frac{6}{7}$ of spine of 1 l.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of spine of 1 l.
	2.	A. Lower border of spine of 12 d.
		B. Junction of upper $\frac{1}{3}$ and lower $\frac{2}{3}$ of interval between spines of 12 d. and 1 l.
	3.	A. Middle of spine of 1 l.
		B. Junction of upper $\frac{5}{8}$ and lower $\frac{3}{8}$ of spine of 1 l.
	4.	A. Junction of upper $\frac{1}{8}$ and lower $\frac{7}{8}$ of spine of 1 l.
		B. Junction of upper $\frac{1}{4}$ and lower $\frac{3}{4}$ of spine of 1 l.
	5.	A. Just below lower border of spine of 1 l.
		B. Middle of interval between spines of 1 l. and 2 l.
	6.	A. Just below lower border of spine of 1 l.
		B. Junction of upper $\frac{1}{6}$ and $\frac{5}{6}$ spine of 2 l.

By carefully examining this table, it will be seen that the superficial origin of any individual spinal nerve has no fixed and definite relation to the apex of one, or the apices of two spinous processes, or the space intervening between two, as one might gather from the tables of Nuhn and Jadelot, but that its position varies considerably.

The following summary may therefore be made of the limits within which I find the posterior and anterior nerve roots take their superficial origin from the cord, in relation to the posterior ends of the spinous processes in the six specimens I have examined (Pl. XIV.):—

(A. Signifies the Highest Point of Origin ; B. the Lowest Point of Origin.)

Nerves.	
2nd Cervical.	A. A little above the posterior arch of atlas.
	B. Midway between posterior arch of atlas and spine of axis.
3rd ,,	A. A little below posterior arch of atlas.
	B. Junction of upper $\frac{2}{3}$ and lower $\frac{1}{3}$ of spine of axis.
4th ,,	A. Just below upper border of spine of axis.
	B. Middle of spine of 3 c.
5th ,,	A. Just below lower border of spine of axis.
	B. Just below lower border of spine of 4 c.
6th ,,	A. Lower border of spine of 3 c.
	B. Lower border of spine of 5 c.
7th ,,	A. Just below upper border of spine of 4 c.
	B. Just above lower border of spine of 6 c.

Nerves.	
8th Cervical.	A. Upper border of spine of 5 c.
	B. Upper border of spine of 7 c.
1st Dorsal.	A. Midway between spines of 5 c. and 6 c.
	B. Junction of upper ⅔ and lower ⅓ of interval between 7 c. and 1 d.
2nd "	A. Lower border of spine of 6 c.
	B. Just above lower border of spine of 1 d.
3rd "	A. Just above middle of spine of 7 c.
	B. Lower border of spine of 2 d.
4th "	A. Just below upper border of spine of 1 d.
	B. Junction of upper ⅓ and lower ⅔ of spine of 3 d.
5th "	A. Upper border of spine of 2 d.
	B. Junction of upper ¼ and lower ¾ of spine of 4 d.
6th "	A. Lower border of spine of 2 d.
	B. Just below upper border of spine of 5 d.
7th "	A. Junction of upper ⅓ and lower ⅔ of spine of 4 d.
	B. Just above lower border of spine of 5 d.
8th "	A. Junction of upper ⅔ and lower ⅓ of interval between spines of 4 d. and 5 d.
	B. Junction of upper ¼ and lower ¾ of spine of 6 d.
9th "	A. Midway between spines of 5 d. and 6 d.
	B. Upper border of spine of 7 d.
10th "	A. Midway between spines of 6 d. and 7 d.
	B. Middle of spine of 8 d.
11th "	A. Junction of upper ¼ and lower ¾ of spine of 7 d.
	B. Just above spine of 9 d.
12th "	A. Junction of upper ¼ and lower ¾ of spine of 8 d.
	B. Just below spine of 9 d.
1st Lumbar.	A. Midway between spines of 8 d. and 9 d.
	B. Lower border of spine of 10 d.
2nd "	A. Middle of spine of 9 d.
	B. Junction of upper ⅓ and lower ⅔ of spine of 11 d.
3rd "	A. Middle of spine of 10 d.
	B. Just below spine of 11 d.
4th "	A. Just below spine of 10 d.
	B. Junction of upper ¼ and lower ¾ of spine of 12 d.
5th "	A. Junction of upper ⅓ and lower ⅔ of spine of 11 d.
	B. Middle of spine of 12 d.
1st Sacral.	A. Just above lower border of spine of 11 d.
5th "	B. Lower border of spine of 1 l.
Coccygeal.	A. Lower border of spine of 1 l.
	B. Just below upper border of spine 2 l.

EXPLANATION OF PLATES XIII., XIV.

PLATE XIII. is an outline drawing, reduced one half, of the dissection described in the text. The specimen was obtained from the body of an adult male, and was hardened in spirit in the horizontal position before the dissection was made. The drawing shows the topographical relation between the superficial origins of the spinal nerve-roots and the apices of the spinous processes of the vertebræ. The nerves and the nerve-roots are coloured *blue* for the sake of clearness, the spinal cord being left white.

PLATE XIV. is a chart showing the variations which existed in six adult specimens between the origin of any given nerve-root and the apices of the spinous processes of the vertebræ. The pale brown areæ on the right side of the middle line represent somewhat diagrammatically the vertical extent of the apices of the spinous processes, without reference to any particular specimen. The blue areæ on the left of the middle line represent the extreme distances, in a vertical plane, within which the individual nerve-roots may arise. It may be observed from this that no one nerve-root has any fixal relation to the landmarks first mentioned.

SUPRA-CLAVICULARIS MUSCLE. By R. W. REID, F.R.C.S.,

Lecturer on Anatomy, St Thomas's Hospital.

IT may be of interest to put on record the occurrence of this somewhat rare anomaly. It was found on the left side of a fairly muscular male subject. It arose by short, flat, and tendinous fibres from the outer border of the medial tendon of the sterno-mastoid and the fascia lata over the immediately adjacent fibres of origin of the pectoralis major, and was inserted by fleshy fibres into the inner inch of the upper surface of the flattened portion of the clavicle, and by short radiating aponeurotic fibres into the deep cervical fascia just above that part of the bone. The muscle was about four and a half inches long, flat and tendinous at each end, and fleshy between. The fleshy part was somewhat compressed from before backwards, and radiated slightly from its sternal towards its acromial extremity. The inner end of the fleshy part measured from above downwards half an inch, the outer end one inch. The greatest thickness from before backwards was half an inch. As regards relations, it lay upon the anterior ligament of the sterno-clavicular joint, the anterior surface of the clavicular origin of the pectoralis major, the upper part of the interval between the pectoralis major and deltoid, the outer three quarters of an inch of the anterior surface of the prismatic portion and the inner inch of the flattened portion of the clavicle. A large branch of the supra-clavicular nerve passed underneath it and sent a good-sized filament into its deep surface.

ABNORMAL DISTRIBUTION OF THE NERVE TO THE QUADRATUS FEMORIS IN MAN, WITH REMARKS ON ITS SIGNIFICANCE. By J. T. Wilson, M.B. Edin., *now Demonstrator of Anatomy in the University of Sydney, and lately in the University of Edinburgh.*

A variation in the distribution of the "Nerve to the Quadratus Femoris" has recently come under my notice in the dissecting room of this University. I have been unable to find any record of the occurrence of the same anomaly, and it is the more interesting in that it finds a parallel in the normal distribution of the same nerve in some of the lower Mammalia.

The condition was substantially alike on both sides of the body, and was as follows:—

The nerve to the quadratus was found to be unusually large, especially on the right side. The usual twigs to the inferior gemellus and the hip-joint were given off, as well as branches to the quadratus muscle, but the nerve itself was found to be prolonged as a considerable branch below the level of the quadratus, and was traced forwards between the obturator externus muscle and the contiguous border of the adductor magnus muscle. On dissection from the front, the nerve was found to enter the anterior aspect of the adductor magnus supplying about two inches of the upper part of that muscle.

The branches of supply from the great sciatic nerve to the adductor magnus were present as usual, and were distributed to its vertical, condylar, portion, while the abnormal branch just described supplied the upper or transverse part of the muscle—usually innervated from the obturator nerve.

It may be well to record the accompanying arrangement of the obturator nerves. On each side the obturator nerve entered the thigh by two divisions, superficial and deep, and there was also present a large accessory obturator nerve in the ordinary position. The superficial division of the obturator nerve was large, and contributed the usual branches to the more super-

ficial adductor muscles, to the femoral artery and the "sartorial plexus," but it continued onwards, still retaining considerable size, and became merged in the long saphenous nerve above the knee.

The deep division supplied the adductor magnus below the area of distribution of the "nerve to the quadratus."

The accessory obturator nerve supplied the pectineus, and, on the left side, it gave off in addition a large branch which entered Scarpa's triangle from beneath the pectineus, and joined the long saphenous trunk.

If inquiry be made into the morphology of the nerve to the quadratus femoris throughout the mammalian series, it will be found that, among the higher orders, it departs only in slight degree from its arrangement in man. In the order Marsupialia, however, it is found relatively larger and more important. In his "Challenger" report on the anatomy of the Marsupials,[1] Professor Cunningham describes the distribution of the nerve to the quadratus femoris in Cuscus as follows:—

> "The nerve to the quadratus femoris sinks into the substance of the gemelli muscles, and is continued backwards through their muscular fibres. Issuing from the midst of the gemellus inferior, it is carried downwards under cover of the quadratus femoris to the adductor magnus. In this course it supplies twigs to the gemelli, quadratus femoris, and probably to the obturator internus, whilst it ends in the adductor magnus, and constitutes its sole nerve of supply."

The arrangement in Thylacine is, according to the same author, practically identical. I find a similar arrangement in *Phalangista vulpina* and in *Dasyurus viverrinus*, so that we may conclude that it is a common arrangement in marsupial animals. In Dasyurus the "nerve to the quadratus" gives off the "nerve to the obturator internus" as a branch, while in Phalangista the latter nerve, though adherent to, may be separated from, the 'nerve to the quadratus," up to their contiguous origins from the ventral aspect of the sacral plexus.

In the monograph above referred to, and in a paper in this *Journal*,[2] Professor Cunningham discusses the bearing of the fact of this distribution of the "nerve to the quadratus" upon the general question of the relation of nerve-supply to muscle-

[1] Page 143. [2] Vol. xvi. p. 1.

homology, and he points out that here we seem to have, so to speak, an invasion of a muscle by the nerve of supply to an adjacent muscle, which militates against the doctrine of immutability of relation between nerve and muscle.

In view of the facts of the case of anomalous distribution of the "nerve of the quadratus" in the human subject, which I have just recorded, Cunningham's objection may be maintained with even greater confidence; for, referring to the ordinary mode of innervation of the adductor magnus in man, he admits that the marsupial arrangement in question

"might be explained by supposing that the adductor magnus is a compound muscle, consisting of a part belonging to the adductor group which in this case has fused with the large adductor brevis, and a part derived from the flexor group, which in the present instance is independent, and receives its nerve-fibres from the same source but through a different nerve-strand, viz., the nerve to the quadratus."[1]

But, at least in the instance of the human variation here noted, there could be no possible confusion between the supply derived through the "nerve to the quadratus" and that derived through the great sciatic nerve, for the branches of the latter were present as usual, and they supplied, as they ordinarily do, that portion of the adductor magnus which arises from the tuber ischii and is inserted into the internal condyle, and which is homologous with the "adductor primus" vel "condyloidea" of some comparative anatomists,[2] whose nerve of supply is the nerve to the hamstrings.[3] The "nerve to the quadratus," on the other hand, supplied the highest portion of the adductor magnus, whose fibres run almost parallel to those of the quadratus femoris.

Further, it must be carefully noted that the condition I have described is not to be confounded with a partial manifestation of a frequently-recorded variety of the quadratus muscle, viz., its fusion with the upper border of the adductor magnus. For (1) the quadratus muscle was normal in size and form; (2) it was, as in the normal subject, separated from the upper border of the adductor muscle by the terminal branch of the internal cir-

[1] "Challenger" *Report*, pp. 143, 144.
[2] Macalister, "Muscles of Edentata," *Trans. Roy. Irish Acad.*, vol. xxv.
[3] So in the Cat.

cumflex artery; and (3) the muscular fibres in question corresponded at their origin with the origin of the adductor magnus, and not with that of the quadratus femoris. Here, then, we have a *triple* innervation of the adductor magnus, and the new element must be regarded as replacing not that usually contributed by the great sciatic nerve, but part of that derived, under ordinary circumstances, wholly from the obturator nerve.

It appears to me, therefore, that Professor Cunningham's suggested solution, in this particular case, of his own objection to the theory of a uniform correlation of nerve and muscle, is insufficient.

SYDNEY, N.S.W.,
8th November 1888.

ON SOME POINTS IN THE ANATOMY OF A *MEGAPTERA LONGIMANA*. By JOHN STRUTHERS, M.D., *Professor of Anatomy in the University of Aberdeen.*

(*Continued from page 335.*)

PART IV.—*continued.*

EAR BONES, MANDIBLE, AND HYOID.

23. EAR BONE—*Tympanic.*—The following are the dimensions of the tympanic bone in Megaptera, and in the 50-feet long B. musculus, in inches:—

	Megaptera.	B. musculus.
1. Length, ...	$4\frac{3}{8}$	$4\frac{6}{8}$
2. Breadth, on posterior third, ...	$2\frac{1}{2}$	$2\frac{1}{2}$
3. ,, on anterior third, ...	2	$2\frac{3}{8}$
4. Height, from tip of lamella before meatus, .	$3\frac{1}{2}$	$3\frac{5}{8}$
5. Breadth of smooth part of inner surface, at middle,	$1\frac{5}{8}$	$1\frac{4}{8}$
6. Width of anterior division of the aperture, .	1	$\frac{7}{8}$
7. ,, of aperture at the division, . .	$\frac{7}{16}$	$\frac{9}{16}$
8. Weight, in ounces, ...	$14\frac{1}{2}$	$15\frac{3}{4}$

The tympanic bone of Megaptera may be distinguished from that of B. musculus by the following characters:—1. It is shorter in proportion to its breadth than in B. musculus. 2. As seen from below, in B. musculus the breadth of the bone at the lobein front of the median constriction on the outer side is nearly as great as at the lobe behind it. In Megaptera the constriction is farther forward, and the breadth is considerably less before than behind the constriction. 3. Viewed from behind,

the surfaces in B. musculus are seen to slope from the inferior border like a gable-roof. This flattening is wanting in Megaptera, the whole of the under surface being convex transversely, except slightly before and behind. 4. Seen on the inner surface, in B. musculus the smooth part is marked off from the rough part by a much more defined border than in Megaptera. 5. This smooth part is more bulged in Megaptera on its posterior half, contributing to the increased breadth on the posterior half of the bone. 6. The aperture is more constricted in Megaptera at the division into anterior and posterior parts. 7. The anterior (Eustachian) division presents marked differences in form. In B. musculus its anterior end bends upwards to a subacute point, so that the lower boundary of the aperture is nearly uniformly concave. In Megaptera the anterior end is directed obliquely downwards and forwards, and is almost square-shaped, so that the lower boundary is convex behind, and then very concave in front. The width of the anterior division of the opening is greater in Megaptera than in B. musculus; greatest width at its posterior half, owing to a bend up of the wall here at the anterior junction with the petrosal, much more marked than in B. musculus. The ridge which here forms the exact upper boundary of this division of the aperture is smooth and concave in B. musculus. It is very thin and sharp in Megaptera, and goes spirally forwards on the smooth surface in front. 8. The width of the posterior (meatus externus) part of the aperture is also greater than in B. musculus, at its last half inch $\frac{1}{8}$ to $\frac{1}{6}$ inch in B. musculus, $\frac{3}{8}$ to $\frac{1}{2}$ inch in Megaptera.

Viewed from the outer side, two depressions are seen, dividing the surface on its upper half into three lobes. The anterior depression corresponds to the constriction between the Eustachian and the meatus divisions of the aperture. The middle lobe is continuous with the broadest part of the bone, and, upwards, there is prolonged from it, at its back part, a flat lamella which projects in front of the external meatus. The third or posterior lobe does not extend so far on the under surface as the other lobes, and is continued upwards to end in a nipple-shaped process, which forms the projecting lower boundary of the meatus externus. 9. In B. musculus the pre-meatus lamella is more bent, sigmoid behind (concavity below the middle). 10. An

antero-posterior depression in front of the base of the lamella, bounding the middle lobe above, is much better marked in B. musculus, cutting the lamella off from the lobe, except behind. 11. The nipple-like process projects more in B. musculus, projecting for $\frac{2}{3}$ the length of the lamella; in Megaptera projecting for about $\frac{1}{3}$ the length of the lamella. The depression between the nipple-like process and the lamella is narrower in B. musculus. 12. The form of the bone behind the nipple-like process is different. There is more of the bone behind the process in B. musculus; but what is most distinctive here is, that the inferior border in B. musculus is carried farther round, to the level of the base of the nipple-like process, and as a thick crest; while in Megaptera the border forms a sharp peak at about the middle of the posterior end of the bone.

Periotic.—In Megaptera, the dimensions of the periotic bone are, in inches—*anterior division*, length $4\frac{1}{2}$, transversely 4, height $2\frac{1}{2}$—*posterior division*, length $7\frac{3}{4}$; height $2\frac{1}{8}$ anteriorly, 5 at the middle; thickness $1\frac{1}{2}$ above, below about $\frac{1}{2}$ inch. The inner surface of the wing-like posterior division is very rough on its upper half; on its lower half it is concave vertically and comparatively smooth, but is again roughened and thickened at the lower free border. The whole external surface is strongly streaked in the direction of the wing, the ridges curved, convexity downwards. The whole wing is slightly bent on its axis, concavity on the outer surface. Upper border a little concave for $4\frac{1}{2}$ inches (then broken for 3 inches), lower border very convex for 6 inches (then broken off). There is no trace of separate development of the upper and lower parts of the wing.[1] The posterior junction between the periotic and tympanic is 1 inch in breadth (outwards and backwards), in thickness $\frac{3}{8}$, thinner behind; the anterior junction is 1 inch antero-posteriorly, in thickness $\frac{1}{4}$ inch in front, $\frac{1}{12}$ inch behind.

Meatus externus and Tympanum.—In Megaptera, the irregularly square-shaped meatus externus, included between the tympanic and periotic and their two junctions, measures, at its *outer end*, vertically 1 to $1\frac{1}{4}$ inch; antero-posteriorly, at the lower part $\frac{7}{8}$ inch, below the middle nearly $\frac{1}{8}$ inch less, owing to the backward curve of the lamella. The upper

[1] See note, page 372.

boundary, formed by the periotic, is a little concave; the posterior boundary, formed by the posterior junction, is a little concave and is smooth; the lower boundary, formed by the tympanic, has projecting into it, for about $\frac{1}{4}$ inch, the nipple-like process. The anterior boundary is formed at its upper $\frac{2}{3}$ by the concave outer edge of the lamella of the tympanic. At the upper $\frac{1}{3}$ of this boundary the bony meatus opens into a fissure, $\frac{3}{4}$ inch long, $\frac{1}{4}$ inch wide, between the periotic and tympanic, closed in front by the hinder edge of the anterior junction, near to which the fissure becomes suddenly narrowed.

The lower bony wall of the *passage*, from its outer end to the posterior division of the opening of the tympanic bone, is short, $\frac{1}{3}$ inch behind, at the nipple-shaped process; in front of this it is a mere edge. The smooth concave surface on the front of the posterior junction is 1 inch in height as well as in breadth, and has that length as a wall of the meatus in to the very back of the opening of the tympanic bone, but about half that smooth surface is external to the plane of the upper boundary. The distances from the outer end of the meatus to the promontory, just below the fenestra ovalis, are at anterior and upper walls of meatus $1\frac{1}{2}$ inches, at posterior wall $1\frac{3}{4}$ inches, taken from the outer edge of the smooth surface. The fenestra ovalis is opposite the upper posterior corner of the meatus externus. It lies at the bottom of a conical recess, about $\frac{1}{3}$ inch deep, into which the stapes is sunk. The stapes moves freely, but it is so held in the fenestra, at the apex of the fossa, that it cannot be removed.

[In *B. musculus* the smooth anterior surface of the posterior junction, bounding the meatus behind, presents a very different character. It forms a deep rounded fossa, about $\frac{3}{4}$ inch in diameter and $\frac{1}{3}$ inch deep, receiving the end of the thumb, and opens in front into the narrow posterior end of the opening of the tympanic bone. In Megaptera the concavity is shallow, about $\frac{1}{8}$ inch deep.]

24. THE MANDIBLE.—The following table (Table II.) brings out various differences on the mandible of the two species. In comparing the form, the parts to be observed are the coronoid process, the condyle, the elongated neck between these two processes, and the body in front of the coronoid process.

TABLE II. *Measurements of the Mandible,* given in inches.

	Megaptera, 40 feet long.	B. musculus, 50 feet long.
*1. Length, in a straight line,	$120\frac{3}{4}$	135
2. ,, along curve, on outer side,	$130\frac{3}{4}$	143
*3. Depth of curve,	$17\frac{3}{8}$	$17\frac{3}{4}$
4. Height, at 6 inches from symphysis,	$6\frac{1}{2}$	7
*5. ,, at middle,	10	9
6. ,, at 12 inches from tip of coronoid,	11	12
*7. ,, at coronoid (body and process),	$12\frac{3}{4}$	17
8. Coronoid process, height behind,	$3\frac{1}{4}$	$8\frac{1}{2}$
9. ,, height in front,	$1\frac{1}{2}$	$4\frac{1}{4}$
10. ,, breadth at base,	7	$8\frac{1}{2}$
11. ,, ,, at mid-height,	$3\frac{3}{4}$	5
12. ,, thickness at middle,	$1\frac{1}{4}$	$1\frac{5}{8}$
13. From top of coronoid to top of condyle,	22	22
14. ,, to end of condyle,	25	25
15. Greatest depth of neck,	$2\frac{3}{4}$	$7\frac{1}{2}$
16. End of condyle to anterior edge of dental foramen,	$11\frac{3}{4}$	16
17. From same edge of foramen to back of coronoid,	9	4
18. Height at anterior fourth of neck,	$9\frac{5}{8}$	$9\frac{1}{4}$
19. ,, at middle of neck,	$9\frac{1}{2}$	$8\frac{3}{4}$
20. ,, at posterior fourth of neck,	$7\frac{3}{4}$	$9\frac{1}{2}$
21. Condyle, height (entire end of bone),	11	$12\frac{1}{2}$
22. ,, thickness, at middle,	6	7
23. Thickness of mandible, near symphysis,	4	$3\frac{1}{2}$
24. ,, at middle,	5	$5\frac{1}{4}$
25. ,, below coronoid process,	$5\frac{1}{2}$	$5\frac{1}{2}$
26. ,, at middle of neck,	5	$4\frac{1}{2}$
For Relation of Mandible to Skull.		
27. From middle of glenoid fossa to end of beak,	117	137
28. From lower part of ditto to ditto,	$120\frac{1}{2}$	140
29. Middle of glenoid fossa to vertical plane of anterior edge of temporal passage,	8	14
30. Ditto to anterior border of floor of orbit,	16	27
31. Projection of mandible beyond beak when condyle is in contact with middle of glenoid fossa,	$2\frac{1}{4}$	2 short

25. CHARACTERS OF THE MANDIBLE IN COMPARISON WITH THOSE OF B. MUSCULUS.

Coronoid Process.—[In *B. musculus* the coronoid process is high ($8\frac{1}{2}$ inches behind, $4\frac{1}{4}$ in front) and curved forwards. The anterior margin has a concavity of about 1 inch deep; the posterior margin is very convex on its upper half, concave (concavity $\frac{1}{2}$ inch deep) on its lower half. The inner surface is nearly flat; the outer surface is concave vertically. The process is moderately everted on its upper half, but mainly owing to the concavity of its outer surface. The outer surface has a strong beam, marking off the anterior third as a deep groove on the upper third of the process, large enough to

receive a large thumb. By means of this beam the process retains its thickness till close to the top. The beam goes nearly straight down, and is lost at the base of the process. The inner edge of the groove is the anterior border of the process, and is continued as the anterior border of the body of the bone. The border of the process is sharp. Just in front of the base of the process the border of the bone becomes rapidly thickened. This *pre-coronoid thickening* extends for about 5 inches, and is then gradually continued on the upper edge of the body. Viewed from the side, this part is slightly convex upwards. The posterior edge of the coronoid process is thin at the middle third, and on about the lower fourth becomes thickened to ¾ inch, as the anterior part of the post-coronoid roughness. The rounding of the top of the process corresponds pretty well to the form of the ends of the four fingers laid together, the fore finger to the front. Viewed from above, the top has a thick, somewhat triangular form, owing to the beam and the groove.]

In Megaptera, besides its much less height than in B. musculus (in Megaptera 3½ inches behind, 1¼ in front), the coronoid process differs in form from that of B. musculus. It is a blunt triangle, the anterior and posterior borders both gently concave till near the top, the anterior the most sloping border, so that the process seems to point a little backwards. It is more everted than in B. musculus, and a little concave on the outer surface. The posterior border of the process is thin throughout (¾ inch, increasing to 1 inch below). The top is less pointed than in B. musculus, and is thick, averaging ¾ inch, more behind, thinner in front. There is no beam on the outer surface, except a little thickening at the top, and consequently no groove on this surface. The *pre-coronoid thickening* is more marked than in B. musculus, 8 to 9 inches in length, in its posterior half 1 inch thick, and raised ½ inch above the level of the border behind and before. It is rough, with an irregular depression dividing it longitudinally, the outer edge of the depression continuous with the anterior edge of the coronoid process. The depression runs back on the inner side of the anterior border of the coronoid, leaving a groove between, which, however, does not correspond to the groove noted in B. musculus.

Neck.—The neck is about the same length in both, but an elevation on the upper border in Megaptera, at and in front of the middle, forms a marked difference, in contrast with the general gentle concavity in B. musculus. This *post-coronoid elevation* is about 7 to 8 inches in length, rising gradually before and

behind to a height of 1 inch above the level of the rest of the upper border of the neck. Viewed from above, it is about 2½ inches thick at the top, narrowing forwards, with a smooth interval, for a hand's breadth, between the elevation and the coronoid process. Backwards the rough surface is suddenly narrowed by the notching to form the dental foramen. The roughness extends down on the inside for 8 inches, in front of the dental foramen, most marked on its anterior 4 inches, where the wall rises as a low mound. The roughness of this post-coronoid elevation is not that of cartilage-covered bone, but as of bone to which tendon or ligament had been attached. The same of the pre-coronoid thickening, but the roughness is less marked.

[In *B. musculus* there is no post-coronoid upward elevation, but on the inside, at this part of the neck, the inward elevation and roughness, over the dental canal, is more marked than in Megaptera. It goes down, for 2½ inches, only to below the level of the middle of the spine, and ends by a well-defined edge. The upper border of the neck at this part, though not forming an upward elevation, is flattened and rough (with a breadth of 1 inch) for 6 inches, being the space between the dental foramen and the coronoid process, the flattening reaching for 2 inches up on the hinder border of the coronoid process. This flattening and roughness of the border here contrasts strongly with the smoothness of this part of the border in Megaptera.]

Direction of the Neck and Position of the Dental Foramen. —The place where the axis of the body and the axis of the neck meet is farther back in Megaptera than in B. musculus. The distance between the back of the condyle and the coronoid process is the same in both (25 inches), but the dental foramen is much further back in Megaptera (11¾ inches from the condyle) than in B. musculus (16 inches). The axes of the body and neck meet at the dental foramen. This gives a very different form to the necks. The outward convexity of the body in B. musculus ceases just behind the coronoid process, and sharply, so that the outer surface of the neck is deeply concave longitudinally (concavity between the coronoid part and the tuberosity below the condyle, 3 inches deep); while in Megaptera the outward convexity of the body goes back to about the middle of the neck, and the concavity is less (about 2 inches deep).

There is also much greater torsion of the neck in B. mus-

culus. In Megaptera the outer surface is directed a little upwards, and is gently and nearly uniformly convex. In B. musculus the upper part of the neck is inclined inwards, the lower part outwards. The whole outer surface of the neck is thus more directed upwards than in Megaptera. Also, in B. musculus the upper half of the posterior third of the neck is concave, and the lower third of the anterior half is flat. This torsion of the neck in B. musculus, mainly from the inward inclination of its upper part and of the base of the coronoid process, is a marked distinctive character. In Megaptera the outer surface of the neck, vertically, remains little different from that of the body till close to the condyle.

Viewed on the inner side, the same difference in the vertical direction is seen, and the axes of the body and neck are seen to meet abruptly at the anterior edge of the dental foramen in B. musculus, while in Megaptera the change is gradual and not great.

Differences at the Dental Foramen.—(1) It is much nearer the condyle in Megaptera; from the back of the condyle, 11$\frac{3}{4}$ inches in Megaptera, in B. musculus 16. (2) As seen from behind, it is on a plane more internal in its relation to the coronoid process in Megaptera. A vertical straightforward plane passing through the outer side of the foramen, in Megaptera passes to the inner side of the coronoid process, in B. musculus intersects the process. (3) The spine, prolonged back from the inner edge of the foramen, is short ($\frac{5}{8}$ inch in length) in Megaptera, in B. musculus long (2$\frac{3}{4}$ inch) and pointed. (4) The notch below the spine goes forward beyond the upper notch, in Megaptera $\frac{1}{4}$ to $\frac{1}{2}$ inch, in B. musculus 2 inches. (5) The groove (about 4 inches long) which ends in the foramen has in Megaptera a broad concave floor, 2 inches broad at the middle, the inner edge raised; in B. musculus it is only 1 inch broad at the middle, and slopes downwards. The wall above the groove in Megaptera slopes upwards and outwards; in B. musculus it is vertical or overhanging. The result is that the groove appears to the eye as if dug out from above in Megaptera and as if dug out from the inside in B. musculus. (6) The foramen is larger in Megaptera, vertically 3 inches, transversely 2$\frac{1}{2}$; in B. musculus it is $\frac{1}{2}$ inch less in both directions. (7) What appears to be the mylo-hyoid groove

is present in B. musculus, running on from the lower notch, for 2 inches as a shallow triangle; it is absent in Megaptera.

Condyle.—The condyle proper is to be distinguished from the more projecting tuberosity below it. The differences on the condyle are—(1) The obliquity, downwards and outwards, is much greater in B. musculus, in adaptation to the corresponding obliquity of the neck, above-noted. (2) In B. musculus the outer edge of the condyle projects forwards, at its lower half, as a broad thick tongue, overhanging the surface of the neck, receiving the finger between them. In Megaptera, although the outer side of the condyle projects more than in B. musculus, there is no abrupt or forward projection, only the thick outer side of the condyle projecting uniformly. (3) The condyle on the inner side in B. musculus projects uniformly, without sharp edge, in its whole height here (about 7 inches). In Megaptera it projects less, has a rough sharp edge at the middle, and is short vertically (about 5½ inches). (4) The groove between the condyle and tuberosity, on the inner side, is in Megaptera situated at the mid-height of the end of the bone, is well defined, large enough to receive the end of the thumb, and is directed obliquely upwards and forwards. In B. musculus it is a wide valley, 4 inches wide, ¾ inch deep at the deepest part, which is some way below the middle of the entire end of the bone. (5) The separating groove on the outer side is also more definitely marked in Megaptera, both above, by the more abrupt projection of the condyle, and below, by the more outward position of this part of the tuberosity.

The differences on the *tuberosity* are not very definite, except in regard to the separating grooves above noted; but it projects more laterally in Megaptera than in B. musculus, both internally, as a sharp forward-ascending edge (entirely wanting in B. musculus), and on the outer side as a broadly-projecting outer edge to the bone below the condyle. In B. musculus it is wanting below the inner third of the condyle; in Megaptera it extends across the whole breadth of the condyle, at the inner part as a narrow ascending edge.

Body.—The proportions of the body of the mandible in Megaptera and B. musculus are seen in the table. The actual *depth of the curve* is nearly the same in both, but as this depth

(17⅜ inches in Megaptera, 17⅝ in B. musculus) is obtained on a shorter jaw in Megaptera (120¾ in Megaptera, 135 in B. musculus) the curving is greater in Megaptera. This is apparent to the eye. The greater width of the jaw in Megaptera and the greater length in B. musculus are apt to mislead the eye in regard to curvature.

In regard to *form*, the body has a thicker appearance in Megaptera on its posterior half, but this is deceptive, being due to the less development of the upper border towards the coronoid process. The thickness of the body is not greater in Megaptera than in B. musculus till near the symphysis. The upper border in Megaptera is gently sigmoid, the convexity on about the second quarter or more. The distal concavity is mainly owing to rising up towards the symphysis, on the last 18 inches.

[In *B. musculus* there is very little of the sigmoid character of the upper border. This is mainly owing to the gradual rising of the border to the high coronoid process, but there is a slight convexity at about the second quarter of the border, and a slight rise towards the symphysis, on about the last 20 inches. The most marked distinction of the body is its greater height on the first quarter in B. musculus, rising gradually to the high coronoid process. This gives the body its general tapering form, modified by the slightly sigmoid upper border.]

There is a difference on the lower border, taking the entire mandible. Owing to the greater descent of the tuberosity, the concavity at the lower border of the neck is much more marked in Megaptera (2 inches deep) than in B. musculus (1 to 1¼ inch deep).

They differ at the symphysis, on the last 6 or 8 inches. In Megaptera the lower border is more sloping; at 12 inches from the end the height is 7 inches in both; at 6 inches, it is the same in B. musculus, half an inch less in Megaptera.

Foramina.—Both series of foramina present differences. The *internal series* in Megaptera, about fifteen in number, open entirely in the groove. They begin 8 inches in front of the coronoid process, 1½ inch below the border, by two or three close together, which rapidly form the groove. After an interval of 18 to 24 inches, a series of foramina open at intervals in the groove, not requiring to ascend to it, except only that the more

posterior open in the lower part of the groove. The groove is not large, wide enough only to lodge the side of the little finger, about $\frac{1}{8}$ to $\frac{1}{6}$ inch deep, and is formed rather of a succession of short grooves continued from the foramina.

[In *B. musculus* the internal series do not begin till about 15 inches in front of the coronoid process, the groove 4 inches earlier. Thereafter there is a continuous groove, formed as in Megaptera, receiving the successive foramina, altogether about 20 in number. There is no wide interval, as there is in Megaptera, between the first group of foramina and those anterior to them. The groove and its foramina are at first rather nearer the border ($1\frac{1}{4}$ inch from it) than in Megaptera, but in B. musculus additional foramina occur farther down. These (2 on the left side, 3 on the right) open at 15 to 23 inches in front of the coronoid process, $1\frac{1}{2}$ inch below the general groove. From each of these a deep groove, wide enough to receive a goose-quill, passes obliquely forwards to enter the general groove, after a course of 7 to 12 inches. The most posterior on the right side again enters the bone, for 3 inches, before it ends in the general groove. These long oblique grooves form a striking distinction of B. musculus from Megaptera.]

The *external series of foramina* are of much greater size, enough to admit a finger somewhat flattened; the internal series vary in size between that of a goose-quill and crow-quill. In both Megaptera and B. musculus the external series are about 6 in number (6 on the right side, 7 on the left, in both), but in Megaptera they do not begin so soon, and are continued further forwards. The distance of the first from the coronoid process is, in Megaptera 32 inches, in B. musculus 24 inches. Thus the internal series begin earlier in Megaptera than in B. musculus; the external series the reverse. The distance of the last of the external series from the symphysis is, in Megaptera 28 to 30 inches, in B. musculus 35 to 38 inches. Owing to their late beginning in Megaptera, the foramina are closer together than in B. musculus. In Megaptera they extend over a distance of 35 to 39 inches; in B. musculus a distance of 54 to 58 inches. They occur at intervals of 6 to 7 inches in Megaptera, of 9 to 10 inches in B. musculus, but with some variation. They are broader and flatter in Megaptera than B. musculus.

At 13 inches from the symphysis (8 to 10 in B. musculus) the dental canal is unroofed by a fissure $\frac{1}{2}$ inch wide all along in Megaptera, much narrower behind in B. musculus. In both, the

groove of the internal series of foramina crosses the top of the bone to join the fissure at its posterior end. Thereafter the upper border of the bone is to the inner side of the fissure. The *mental foramen* is incomplete above, and in Megaptera also in front, but is well defined on its floor at about 2 inches from the symphysis. It is larger in Megaptera (height 1¾ inch) than in B. musculus (height 1¼ to 1½ inch). In Megaptera it occupies more than the upper third of the symphysis, in B. musculus scarcely more than the upper fourth.

26. RELATION OF THE MANDIBLE TO OTHER PARTS OF THE SKULL.—When the condyle is placed in contact with the middle of the glenoid cavity, the tip of the coronoid process of the mandible is, in Megaptera, about 15 inches in front of the anterior border of the temporal passage, and about 2 inches in front of the ant-orbital process of the maxillary. Even with the mandible placed thus far back, the coronoid process would quite clear the orbit and ant-orbital process of the maxillary in the closing of the mouth.

[In *B. musculus*, when the condyle is similarly placed in contact with the glenoid cavity, the coronoid process stands below the orbit, behind the middle of it, and could not but strike the malar bone in the closing of the mouth. In order to enable the coronoid process to clear the ant-orbital prominence, the condyle would have to be advanced from the glenoid cavity for about 15 inches. In the 64 feet long B. musculus I found adhering to the condyle a temporo-mandibular cushion, 30 inches in length, 24 in breadth, 15 to 18 in height (this *Journal*, vol. vi., 1871, p. 123). How much of this lay between the glenoid cavity and the condyle I was unable to note, the mandible having been already detached.]

As the position of the mandible with the condyle in contact with the middle of the glenoid cavity would give a projection at the symphysis of only 2¼ inches beyond the beak (and would in B. musculus place it 2 inches short of the beak), it is evident that there is naturally a considerable interval between the glenoid cavity and the condyle. If the temporal muscle goes to the coronoid process in Megaptera it will, after turning round the anterior boundary of the temporal passage, have a long way to travel, and that by passing close below the soft parts of the orbit. Dissection of the muscles and other soft parts here is necessary to the interpretation of the bone at and near the coronoid process.

27. HYOID BONE.—TABLE III. *Measurements of the Hyoid Bone,* in inches :—

		Megaptera.	B. musculus, 50 feet long.
1.	Extreme width,	22¼	27
2.	At middle of body, breadth (ant.-post.)	5	5½
3.	,, thickness,	1⅜	1¾
4.	Breadth of great horn, at middle,	3	3¼
	,, on outer end,	2½	2½
5.	Thickness of ditto, at middle,	2¼	3
6.	,, on outer end,	2	1⅞
7.	Stylo-hyal, length,	12	14
8.	,, greatest breadth,	2½	2⅞
9.	,, thickness at same part,	1½	1½
10.	,, both ends,	1⅞ × 1	...
11.	,, thick end in B. musculus,	...	2½ × 1¾
12.	,, flat end in ditto,	...	2½ × ⅞
13.	Weight of united body and great horns, in ounces,	48½	73
14.	,, of the stylo-hyals together,	20½	30½

28. CHARACTERS OF THE HYOID BONE, IN COMPARISON WITH THOSE OF B. MUSCULUS.—Although the hyoid bone of B. musculus strikes the eye as larger and more massive than that of Megaptera, it would not be so were we to go merely by the comparative length of the two skeletons. But there are differences in form.[1]

Both ends of the stylo-hyals are flat in Megaptera, while in B. musculus the ends differ materially in thickness, as seen in the measurements given in the Table. The anterior conical processes, commonly regarded as outgrowths from the body, but in the position of the cerato-hyals of other Mammalia, are much

[1] The hyoid of Megaptera is at once known from that of *B. borealis* by the broad stylo-hyals of the latter; also by characters of the body and great horn, especially by the flatness of the great horn in B. borealis. In this 35-feet-long B. borealis the stylo-hyals have not attained the breadth figured by Flower, from the Leyden (Java) finner (*Proc. Zool. Soc.*, 1864, p. 406), and figured, from the same skeleton, by Van Beneden and Gervais (*loc. cit.*, pls. xiv., xv. fig. 28, B. Schlegelii). The vertebræ and other characters figured in that plate leave no doubt that their B. Schlegelii is the same species as my B. borealis. The stylo-hyals in my B. borealis are liker those figured by Van Beneden and Gervais (pls. x., xi. figs. 15, 16, "d'après le squelette de Leide") in their so-called B. laticeps, except that in mine the lower end is more pointed. In this 35-feet-long B. borealis the greatest breadth of the stylo-hyals is 4 inches; length 18, the broad part 9½, the tapering lower part 5 inches.

longer and more robust in B. musculus than in Megaptera. The great horns show a difference in the presence in B. musculus of a fusiform enlargement about the middle. This is better seen on viewing them from behind than from below, as it is mainly on the thickness, vertically, that the enlargement occurs. As seen from the Table, in B. musculus the breadth, from the middle of the horn to the outer end, diminishes by ¾ inch, the thickness by over 1 inch; in Megaptera the breadth falls by ½ inch, but the thickness by only ¼ inch. The diminution in the thickness strikes the eye even more to the inside of the fusiform enlargement in B. musculus.

The appearance of greater up-turning of the great horns in B. musculus (depth of the arch of the hyoid in B. musculus 7¼, in Megaptera 4½ inches) is mainly owing to their greater length in B. musculus; but when viewed from behind, as when laid on the table, resting on the ends of the great horns, the arch in B. musculus is seen to be more acute. This is seen alike on the under surface, the transverse arch being considerably flatter in Megaptera than in B. musculus.[1]

The stylo-hyals in this Megaptera are very like those figured by Van Beneden and Gervais (*loc. cit.*, pl. xi. fig. 7) from their Megaptera Lalandii. The ends of the stylo-hyals and of the horns are incompletely ossified both in Megaptera and in the B. musculus.

[1] It may be noted here that, although the hyoid of the Finners is sometimes drawn and described as if the great horns have a direction backwards from the body, it is not so in any of my specimens. That appearance depends on the position from which they are viewed; but if the under surface of the body is taken as horizontal, the great horns have very little, if any, direction backwards. This is seen by placing the series on a table. The hyoid of Megaptera, B. musculus, B. borealis, and B. rostrata all stand on their posterior border, and the body rises vertically, or very nearly so, from the table. The great horns in B. musculus have at first a slight direction backwards, and rather curve forwards again as they turn up.

This relation of the great horns to the body appears to be a character of these Finners in contrast with Mysticetus. In four great hyoids in my possession, without history (picked up on the shore of the Greenland seas), but which I believe to be those of Mysticetus, the backward direction of the great horns is very marked. When these hyoids are placed on the table so that the body rises vertically, the great horn and body form an arch 4½ to 6 inches in height; and when the bone is laid on its posterior border, the body slopes forwards at an angle of 40° or more.

Note on Dr Gray's Megaptera Novæ-Zelandiæ.—The form of the posterior division of the periotic bone is of particular interest, as the late Dr J. E. Gray founded a new species, Megaptera *Novæ-Zelandiæ*, on the expanded form presented by that part of the bones of the ear sent from New Zealand, and preserved in the British Museum (*P. Z. S.*, 1864, p. 207, and *Cat. of Seals and Whales in Brit. Mus.*, 1866, p. 128, with two figures). He remarks:—"The bones attached to the tympanic are broad and expanded, very unlike the same bones in the Greenland species." In his figure of the bone of the right side seen from without, the posterior part is represented as a square-shaped expansion, length about twice that of the tympanic, breadth equal to the length of the tympanic. In the figure of the ear-bone of Megaptera longimana given by Van Beneden and Gervais (*loc. cit.*, pls. x. and xi., fig. 7), this process is represented, as they describe it, "à peine plus longue que la caisse elle-même" (Text, p. 126; see also references on pp. 119, 134, 135), while Dr Gray's Megaptera Novæ-Zelandiæ "est remarquable par la longueur extraordinaire d'une de ses apophyses." The seemingly conical form of the process in the figure of Van Beneden and Gervais, above referred to, is owing to its being viewed from the inside and above, showing only the thick upper border of the process. That is seen on placing my specimen in the same position; but in my specimen, as in Dr Gray's figure, the process is nearly twice the length, and otherwise corresponds very closely to Dr Gray's figure, making due allowance for the evidently broken-off corners of the end of the wing. The lower corner, especially, is broken off obliquely, giving the end of the wing a bluntly triangular form instead of the squared end in Dr Gray's figure. Making allowance for this, the resemblance to Dr Gray's figure is striking. Even with these mutilations at the end, this wing-like process has a length not far from twice that of the tympanic, and a breadth (height) greater than the length of the tympanic.

It will be borne in mind that we know nothing of the habitat of this Megaptera, or as to whether it was migrating southwards or northwards. Simply that it appeared on the east coast of Scotland about the middle of November, remaining through December, and that Megaptera is very rare on British coasts.

As Dr Gray's New Zealand species is founded on only one specimen, and that of the ear-bone only, it is evident that further observations are required on the form of this part of the skull of the Megaptera of the Greenland seas and of other seas. It has to be determined whether the supposed specific difference, remarkable as it is, may not be a matter of age, or of non-union of the two parts from which this portion of the ear-bone is developed, or of variation within the same species, or possibly of the mutilation of the thinner part in detaching the bone. But should this wing-like expansion of the periotic bone prove to be diagnostic of the Megaptera of the South Pacific, then it must be held that we have here a specimen of the Megaptera longimana of New Zealand migrated thus far northwards.

OBSERVATIONS ON THE ANATOMY OF THE PROSTATE. By JOSEPH GRIFFITHS, M.B., C.M. Edin., *Assistant to the Professor of Surgery in the University of Cambridge.* (PLATE XV.)

(Read at the Meeting of the Anatomical Society, Feb. 6, 1889.)

BEFORE the discovery of the "third lobe" of the prostate, announced to the Royal Society by Sir Everard Home in the year 1806, there was no explanation of the occurrence of an enlargement of this part of the prostate, which had been observed and found to be the cause of considerable difficulties in micturition in old men.

Home's discovery was accepted by most anatomists and surgeons of this country; but amongst the French there were many who did not regard the "third lobe" as an extra lobe, and who considered it as a part of the gland placed in the middle line, posteriorly, between the vasa deferentia so constituting a "middle part."

However it was not until Sir Henry Thompson took up the study of the prostate, from an anatomical and pathological point of view, that any real doubt was thrown upon Sir Everard Home's discovery.

After considerable investigation into the literature, I came to the conclusion that the subject is in a very unsatisfactory state, and determined to enter upon an inquiry for myself.

Before proceeding further, I may here quote what Sir Everard Home said in his communication to the Royal Society:—

"On turning back the vasa deferentia and the vesicula seminales, we came down upon a rounded prominent body, exactly in the sulcus, between the lateral lobes of the prostate; it was embedded under their rounded termination, and adhered to the coats of the bladder; its circumference could not be distinctly seen till the ends of the lateral lobes were detached, and when this was done the continuity of the glandular structure could be readily shown on the side next the bladder; the ducts passed directly through the membrane of the bladder. This lobe completes the circular ring through which the tube of the urethra passes" (*Phil. Trans.*, 1806).

Although much has been written on this subject since, the only observations of importance are those of Sir Henry Thompson, who conducted a series of investigations into the normal as well as the pathological conditions found in this gland. His results were fully brought together and published in the *Jacksonian Prize Essay* for 1859, in which I find the following conclusion:[1]—

> "I cannot find in healthy bodies, below fifty years of age, any formation in the situation described capable of being recognised as a distinct 'third' or 'middle lobe,' and am compelled to conclude that any marked prominence there, which appears to possess independent characters (as regards size or form), must be considered abnormal or morbid."

I gather from the preceding remarks that Sir Henry Thompson could not confirm the observations made by Sir Everard Home. He, however, endeavours to explain the existence of a "third lobe" by referring it to the pathological field, as Morgagni and others had previously done.

For the purpose of clearing the anatomical ground, I investigated all normal human prostates that came in my way; and, although the number is limited, still the observations are, I think, worthy of notice. I have followed in my investigations two plans—(1) to observe, after opening the urethra from the front, the position of the orifices of the prostatic ducts; and (2) to make median longitudinal sections of the gland after hardening in spirit, as I find that method gives more reliable and satisfactory results than section of the fresh gland.

I find that in a certain number of individuals, of whatever age, there are numerous orifices of prostatic ducts in the part of the urethra between the posterior end of the verumontanum and the vesical orifice in addition to the usual linear series, on either side, in the prostatic sinuses. In some instances the duct-orifices in this first part of the urethra are numerous (ten or twelve), easily detected, and arranged more or less in a concentric form, as diagrammatically represented in the accompanying figure. The secretion may be seen oozing from these orifices when the median part of the prostate behind the verumontanum is pressed. I judged that ducts opening in this situation would

[1] In his later writings the same views are held.

probably be derived from the portion of the gland called the "third" or "middle lobe."

To corroborate this view, I made median longitudinal sections in the specimens in which these orifices existed, and found, in each case, a portion of prostatic tissue of variable size occupying the situation assigned to the "third lobe."

All the cases which I allude to as presenting these appearances were in young and middle-aged persons: one was a boy twelve years of age. The presence of the "third lobe" cannot, therefore, be regarded as pathological; and I repeat, that it only exists in a certain number of individuals.[1] The relative frequency of its occurrence I have not been able to determine, as my material is limited; but, from my opportunities, I am inclined to think that a certain amount of gland tissue exists in this situation in most instances.

In the cases in which the "third lobe" is pronounced it forms a rounded mass, possessing a capsule, derived from and continuous with that of the rest of the gland; and leading from it into the vesical end of the prostatic urethra, as I have just said, are ducts similar to the other prostatic ducts. These form the excretory channels of this portion of the gland.

It is indeed clear that this part of the prostate, with its separate ducts, is in some instances in normal conditions developed to such an extent as to render it quite worthy to be called a "third or median lobe."

My observations thus to some extent confirm those of Sir Everard Home, but I find that in some individuals it is absent, and that there is every gradation up to the size which he represents.

It has, as we have already seen, been suggested that the "third lobe" consists of an extension of the lateral lobes backwards to the space between the vasa deferentia; but that it is as real a part as either of the lateral lobes is proved by the exist-

[1] I especially wish to draw attention to this point, and to remark in passing, that it follows that enlargement of the third or median lobe of the prostate does not and cannot take place in those individuals in whom the gland tissue in that situation is absent. Indeed, it is the presence or absence of gland tissue in the situation assigned to the third lobe that determines the presence or absence of enlargement in that position, in cases of general enlargement of the gland; this is also true of the part of the gland in front of the urethra. See further on.

ence of ducts belonging to it, and by the fact that the position of outlet of its ducts is different from those of the lateral lobes.

Reference will be made in a subsequent paper on the enlargement of the prostate, to the existence of the ducts from the "third lobe"; and their importance in the pathology of the gland will be then discussed.

In examining the prostates of man and the lower animals, I have been struck with the regularity with which numerous venous channels, almost amounting to a plexus, are found in the anterior wall of the prostatic urethra. These venous channels are more numerous towards the middle of the prostate, and they are placed immediately subjacent to the mucous membrane in the somewhat dense submucous tissue, being only covered by the epithelium. Cases in which the veins become full previous to or during the death of the individual, show these venous channels very well, and they then form dark lines running more or less parallel to one another in the direction of the urethra. I have not yet been able to investigate them any further, and here merely wish to draw attention to the existence and very superficial position of these venous channels. These, in addition to similar, though less numerous and less prominent, veins in the hinder wall, and which are in like manner situated immediately beneath the epithelium near to the neck of the bladder, explain the easily excited and considerable hæmorrhage from the prostatic urethra, of not unfrequent occurrence, after the passage of instruments.

Minute Anatomy.

The general anatomy of the prostate is so well known, that all I propose is to briefly describe the main features in the histology of the gland.

The normal histology of the prostate was carefully studied and described by Kölliker; and a very clear description is given in Klein and Noble Smith's *Atlas of Histology*, and indeed by many other writers.

A *transverse section* near the middle shows it to consist mainly of a mass of gland tubules surrounded by a distinct strong fibrous capsule, which is connected on its inner aspect with trabeculæ separating and supporting the glandular divi-

sions. Near the middle of the section is seen the crescentic urethra, and below or behind it is a dense mass, consisting of connective tissue, with a few non-striped muscle fibres, traversed by gland "ducts." There exist very few, if any, gland "tubules" in this situation. From this central mass of tissue strong trabeculæ, similar to those just mentioned, pass outwards towards the periphery to join the capsule; they in their turn give off smaller trabeculæ of similar structure, which invest the terminations of the gland tubules. The trabeculæ thus all radiate from the dense tissue behind the urethra; and with reference to this it may be remarked that, as I show later on, the prostate in man originally develops at this hinder part, and subsequently, up to the period of adolescence, extends laterally and forwards round the sides of the urethra, to meet ultimately in the middle line anteriorly. The gland is of the usual compound tubular type, and the tubules, which open by means of short ducts upon the floor of the urethra, branch and reach to near the periphery. In favourable sections they may be seen in their entire extent.

The "ducts" do not possess any special coats of their own beyond the columnar epithelium which lines them; and they constitute mere channels embedded in the supporting structure at the back of the urethra already referred to.

The "tubules" and their continuations or secreting portions of the gland are lined by long and slender columnar cells, each cell possessing an oval nucleus placed near the attached end. The protoplasm of the cells, towards the lumen of the tubule, is usually found to be very granular, and the cells to have no well-defined free border. Between the attached extremities of these columnar cells small pear-shaped cells[1] are not unfrequently seen, which rest upon the basement membrane of flattened epithelial cells. This basement membrane, which is present throughout in the gland tubules, is separated from the surrounding network of capillaries by a thin homogeneous layer. In some places, where the epithelial cell-lining has fallen away during the manipulation of the section, may be seen the basement membrane of flattened epithelial cells, proliferating and giving rise to the small pear-shaped cells which are ultimately developed into the columnar cells (see Pl. XV. fig. 3).

[1] These small pear-shaped cells were first described by Langhans.

The character of the epithelial lining remains much the same from the extremities of the gland tubules to the beginning of the ducts. In the ducts, which are very short, a gradual change takes place between the epithelium lining the tubules and the transitional epithelium lining the prostatic part of the urethra.

The supporting structure, or stroma, consists of connective tissue, in which there are found many non-striped muscle cells arranged in bundles, and crossing one another in various directions. These muscle-bundles are chiefly disposed around the peripheral parts of the tubules, and their contraction compresses the tubules, forcing the secretion towards the urethra (see Pl. XV. fig. 4). In the stroma there are, besides, the blood-vessels and nerves belonging to the gland.

The Utriculus Masculinus.

In the *utriculus masculinus* the mucous membrane is thrown into folds, and bears on its surface columnar cells. The submucous coat consists of somewhat loose connective tissue which supports numerous thin-walled blood channels (spaces lined with a single layer of flattened epithelial cells). Externally is a thin layer of circularly disposed non-striped muscle.

The *utriculus* constitutes a separate structure, which is distinct from, and merely becomes surrounded by, the prostate in the course of its growth.

The Arrangement and Origin of the Muscular Element of the Prostate.

The arrangement of the muscular fibres in the prostate, and the relation that exists between them and the muscular coats of the urethra, are subjects surrounded with difficulties, so long as investigations are confined to the adult.

During the development of the prostate gland from birth to adult life, the—originally simple—arrangements become changed and more complex, and so obscured that it ultimately affords no clue to the original source and arrangement of the muscle. With the hope of elucidating these points, I examined microscopically a series of sections taken, at intervals of an ⅛ of an inch, from the neck of the bladder down to the anterior ex-

tremity of the prostate in a fœtus nine months old. It would facilitate the description of the muscular fibres if I first give a brief account of the development of the gland.

At the time of birth the prostate forms a small mass, slightly divided into two lateral lobes, situated almost entirely behind the level of the urethra; and it then consists of a number of gland tubules with short branches embedded in a connective tissue stroma rich in non-striped muscle cells. These comparatively simple tubules are derived from outgrowths of the epithelium forming the hinder wall of the urethra, especially from those parts on either side of the *verumontanum*, namely, the prostatic sinuses.

The portion of the urethra from which the tubules originate, it will be remembered, is formed from the part of the wall of the *uro-genital sinus* in the immediate neighbourhood of the orifices of the primitive *genital ducts*, both Müllerian and Wolffian.

Therefore the prostate is in reality derived from outgrowths of the epithelium lining the original *uro-genital sinus* after the manner of other glands, and is not, as has been supposed, and is indeed now very commonly believed, derived from some part of the lining of the *Müllerian ducts*.[1]

The gland tubules grow at first backwards, then outwards and forwards into and between the fasciculi of the thickened posterior half of the external circular non-striped muscle-coat of the urethra in this situation presently to be described.

The growing tubules further divide, and become more and more branched, until their full development of the gland is established. And as these gland-tubules grow forwards on each side, they nearly or quite meet in the middle line in front of the urethra. In some instances the gland substance from the two sides fuses together in front, but in others it fails to do this, and an interval between the two sides is left. Hence the amount of prostatic

[1] It would follow, therefore, that any structure in the female homological with the prostate in the male, must be sought near the fore part of the urethra and in its immediate neighbourhood in the small mucous glands which are there found. Sir J. Y. Simpson expresses the same view in his article on "Hermaphroditism" (*Anæsthesia, Hospitalism, and other papers*, p. 509), as follows:—"And if we are to find a true prototype in the female of the prostate gland in the male, we shall probably detect it in the follicular glands and structures that exist so abundantly in the course and at the extremity of the female urethra."

tissue in front of the urethra varies considerably in different individuals.

The third or median lobe develops in like manner when present by extension backwards of the tubules originating behind the *verumontanum.*

To return to the muscular coats of the urethra. The external or longitudinal coat of the bladder (*detrusor urinæ*) terminates by insertion into the base of the prostate at or near the vesical orifice of the urethra.[1] The circular coat suddenly diminishes in thickness just below the neck of the bladder, at the commencement of the urethra, and may be traced onwards as the *external, circular, non-striped muscle* coat of the urethra. The latter, however, differs from the circular coat of the bladder in having its bundles more closely packed together to form a denser layer. This difference is marked to the naked eye both in the male and female urinary organs.

At the level of the *verumontanum,* in the prostate of a fœtus at nine months, this circular coat is seen as a continuous sheet along the anterior wall of the urethra, whereas at the sides and posteriorly it spreads out into slender fasciculi, which invest the developing tubules of the prostate. It undergoes a special thickening in this region behind the *verumontanum,* where the developing tubules of the prostate grow out from the urethra; and the fasciculi derived from this part, and accompanying the tubules in their divisions constitute the muscular element of the prostate. Thus the muscle-fibre and gland-tubules grow on together, the former accompanying the latter in their whole extent, so that the muscle fibres form an investment to the gland-tubules to their very extremities. The gland-tubule-growth, however, exceeds that of the muscle-fibre, so that the glandular constituent forms a relatively and gradually increasing element of the organ. It is further to be observed that the "*ducts*" or excretory parts of the prostatic gland-tubules are devoid of a muscular investment; this results from the fact that these "*ducts*" occupy the situation near the *verumontanum,* between the mucous lining of the urethra and

[1] In the female the external longitudinal muscle-fibres of the bladder are inserted into the external fibrous coat of the urethra, immediately below the neck of the bladder.

the circular coat, in which situation there is, in the early fœtal state, a considerable quantity of connective tissue. Hence the developing ducts traverse this tissue before reaching the circular muscle-coat of the urethra and acquiring from it their muscular sheath.

Internal to the above described circular muscle-coat of the urethra, which, as just said, is continuous with the circular coat of the bladder, is an imperfect coat of longitudinal muscle-fibres which run in separate bundles. This is thickest posteriorly in the *verumontanum*, and there encloses the *utriculus masculinus* Internal to it, and separated from it by a thin layer of connective tissue, is a thin compact layer of circular muscle-fibres in the connective tissue immediately subjacent to the epithelium lining the urethra.

There are, therefore, three layers of muscle in the urethra,—an internal, circular, immediately beneath the mucous membrane, or forming its deeper part, and constituting a *muscularis mucosa;* a middle, longitudinal, the bundles of which scarcely form a continuous sheet (it is possible that this is continuous with the obliquely longitudinal inner muscular fibres of the bladder, but I have not been able to satisfy myself that such is the case); thirdly, an outer, circular, coat, which is the continuation of the circular muscle coat of the bladder into the urethra. These three layers, it will be noticed, are quite distinct from the "*external sphincter of Henle,*" which is composed of *striped* muscle (continuous with the striped muscle around the membranous urethra), and covers the fore part of the prostate, and beneath which the prostate in its development extends itself (see Pl. XV. fig. 5).

In the adult, a thin layer of non-striped muscle immediately surrounds the gland, which does not appear to have any direct connection with the circular muscular coat of the bladder, and which is situated beneath the *striped* muscle of *Henle*—in fact, forming a part of the capsule. From it fasciculi pass between the larger divisions of the gland, and these again are continuous with the muscular fibres investing the ultimate groups of tubules, and which are developed from the outer circular layer of the urethra in the manner already described.

If a group of tubules be examined, it will be seen that the

muscular fibres in relation to them are arranged around the tubules in such a manner that their contraction exercises compression on the extremities of the tubules, and so forces out into the urethra the secretion contained in their interior.

These observations regarding the muscle element of the prostate are not in accord with the view put forth originally by Mr Ellis in the *Med. Chir. Trans.*, vol. xxxix., and since adopted by Mr Harrison of Liverpool (*Surgical Diseases and Injuries of the Urinary Organs*).

The following are extracts from Mr Ellis's paper:—

"The prostate is essentially a muscular body, consisting of circular or orbicular involuntary fibres, with one large hole for the passage of the urethra.

"Its [prostate] circular fibres are directly continuous behind, without any separation, with the circular fibres of the bladder; and in front a thin stratum, about $\frac{1}{80}$th of an inch thick, is prolonged forwards from it around the membranous part of the urethra, so as to separate this from the surrounding voluntary constrictor. Within, and quite distinct from the circular fibres, lies the tube of the urethra encased by its submucous layer of longitudinal fibres.

"I would propose the name '*orbicularis vel sphincter urethræ*' for both the prostate and the prolongation around the urethra."

1st. I do not find that the prostate is essentially a *muscular* organ, but essentially a *glandular* organ, and that the muscle-element is secondary in importance.

2nd. I do not find any of the muscular fibres of the prostate are *directly* continuous with the circular coats of the bladder, but that they are the resultant of an outgrowth of the external, circular, muscular fibres of the urethra upon the prostatic glandular tubules, and are, therefore, only *indirectly* continuous with the circular fibres of the bladder. This applies to the enveloping fibres of the prostate as well as to the fibres in the interior of the gland.

3rd. On this view, the term "orbicularis vel sphincter urethræ" is hardly applicable.

In the present paper I merely describe the structure and the intrinsic muscle of the prostate, and I have not entered into the consideration of the extrinsic muscles, such as the *external sphincter of Henle* and *levator ani*, which in their contraction compress the prostate forcibly, and so serve

the purpose of ejaculating the urinary, seminal, and prostatic fluids from this capacious tract of the urethra.

It appears to me that the predominance of the muscle-element in the prostate has been much exaggerated. The muscle-cells and fibres are considerably more numerous than in other glands, but they are arranged in the main around the extremities of the tubules, and even there do not by any means preponderate over the glandular parts. The general disposition of the muscle upon the tubules, and the absence of any muscular coat to the excretory ducts, are characteristic features of this gland, and may, I think, be considered to have relation to the function of the gland as an accessory to the sexual organs.

The requirements in relation to that function are not continuous, but very occasional; and the muscular fibres are disposed in such a manner that, by simultaneous action, they may produce a more or less rapid expulsion from the tubules, through the ducts into the urethra, of the secretion formed in the tubules of the gland.

The chief conclusions arrived at in this paper are the following:—

1. The *third or median* lobe exists, in many instances, as a well-defined portion of the gland at the time of puberty and during adult life, *i.e.*, the period before enlargement of the prostate occurs, but in other instances it is very small or entirely absent.
2. This part or lobe possesses ducts of its own, which open upon the parts of the hinder wall of the prostatic urethra, which extends from the vesical orifice to the *verumontanum*.
3. This part or lobe also develops separately from the part of the urethra just mentioned, in the same way as the lateral lobes do from the part of the urethra on each side of the *verumontanum*, and it is not the result of an extension backwards of gland tissue from the lateral lobes into the interval between the vasa deferentia beneath the neck of the bladder.
4. The whole gland is peculiar in this particular, that the "ducts" are short, and form mere channels in the stroma, being destitute of any special coats except a layer of

epithelium lining them, and that the muscle tissue of the prostate is so arranged around the terminations of the "gland tubules" which form the secreting parts, that the muscle, when it contracts, is able to act as an efficient expulsor along the whole course of the tubules.

5. This arrangement of the muscle in the prostate is developed in relation to the function[1] of the gland; and thus it is that the secretion accumulated in the tubules can be completely expelled into the urethra at once, or at least in a short time.
6. The muscle-element of the prostate is derived from the outer, circular, non-striped muscle-coat of the prostatic urethra, this coat being continuous with the circular coat of the bladder; therefore the muscle-element of the prostate is only indirectly continuous with that of the circular coat of the bladder.
7. The *utriculus masculinus* is not, properly speaking, embedded in the prostate. It forms a distinct structure separate from the prostate; and as the growth of the prostate greatly exceeds that of the *utriculus masculinus*, the latter is in time covered in, and appears as if embedded in the former.

DESCRIPTION OF PLATE XV.

Fig. 1. Diagrammatic representation of the hinder wall of the prostatic urethra seen from the front, to show the position of the orifices of the prostatic ducts. (*a*) Orifices of ducts from the third or median lobe; (*b*) orifices of ducts from the lateral lobes; (*c*) verumontanum, with opening of utriculus masculinus.

Fig. 2 is from a median section of the prostate of a young adult, and in which the "third lobe" is very prominent.

Fig. 3. Section of the prostate of a man, 30 years; × 400 (Camera Lucida). (*a*) Columnar epithelial cells, with nuclei near attached ends; (*b*) nuclei of small pear-shaped cells between attached extremities of columnar cells; (*c*) flattened layer of epithelial cells, forming a basement membrane, and from which the small pear-shaped cells are formed.

[1] The function of the prostate being glandular, and accessory to the true generative glands.

Fig 4. Section of the prostate of a child five years old, × 40 (Camera Lucida). (*a*) Developing prostatic gland tubules; (*b*) the connective tissue stroma; (*c*) muscle fibres disposed around the developing tubules.

Fig. 5. Transverse section through the middle of the prostate and urethra in a fœtus æt. 9 months; × 20 (stained with picrocarmine). (*a*) urethra; (*b*) utriculus mas. and vasa deferentia; (*c*) muscle enclosing them; (*d*) developing prostatic tubules; (*e*) external sphincter of Henle; (*f*) external non-striped muscle-coat of the urethra in front, and spreading out to form the muscle of the prostate laterally and posteriorly; (*g*) bundles of internal longitudinal coat; (*h*) internal, circular, non-striped muscular coat of urethra; (*i*) submucous veins in superior and anterior wall of urethra.

OBSERVATIONS ON THE ANGLE OF THE NECK OF THE THIGH-BONE. By Professor HUMPHRY. (PLATES XVI., XVII., XVIII., XIX.)

THE photographic representations in Plates XVI., XVII., XVIII., and XIX. are chiefly from specimens mentioned in my paper at page 273 of this volume of the *Journal*. They are all in the Cambridge Museum.

Fig. 1 is the section of the upper part of the thigh-bone of a woman, reported to be 103 at the time of her death. The angle is a fairly wide one, affording no probability of its having decreased with advancing years; but the bone shows well, by its contrast with a similar section of an adult femur (fig. 2), the changes incidental to age. It is remarkably light. The whole femur, though it is a large and well-formed bone, weighs only five ounces, the reduction in weight having been caused, not by any removal from the exterior, and any reduction of size, but by absorption in the interior affecting the cancellous texture and commencing in the finer parts of that texture and, then, invading the coarser plates and the inner layers of the bone-wall. The more delicate plates of the cancelli have been quite cleared away; the stouter arches supporting the outer part of the upper wall of the neck are gone, and the still denser plates descending from the upper surface of the head to the inner wall of the shaft, in the axial or weight-bearing line, are much reduced in number and size. Further, the outer wall of the bone is reduced to an almost egg-shell-like tenuity, and can scarcely be traced over the great trochanter. No wonder that in such condition fracture easily occurs in the expanded and cancellous parts of the bone, that a slight blow upon the hip, a mere turning upon the hip in bed, as one specimen in the museum shows, may cause fracture and driving of the neck into the delicate fabric of the trochanter, or that a sudden impulse of the pelvis upon the head, as in a slip off the kerb-stone, may break the head off from the neck. In short, it is the absorption of cancelli, reducing the strength of the end of the bones in greater proportion than that of the

shafts, which causes the great liability to fracture near the joints in old people.

Fig. 3 is the skeleton of the child with hydrocephalus (p. 278), in which the angle of each neck of the thigh-bone is 148°. The photographic representation scarcely gives an adequate idea of the thinness of the limb-bones.

Fig. 4 is the upper part of the thigh-bone, with an angle of 143°, from a paralytic limb, removed at the hip-joint in consequence of disease at the hip (p. 279). The circumference of the head of the bone is 5⅛ inches; the length of the bone is 15½ inches

Fig. 5, with an angle of 130°, is judged to be also from a paralytic limb. The circumference of the head of the bone is 5¼ inches; the length of the bone is 15½ inches.

Fig. 6, with an angle of 150°, also judged to be from a paralytic limb. The circumference of the head of the bone is 5⅛ inches. The shaft is thinner than might be inferred from the view of the upper part, which is flattened. The bone measures 16 inches.

In each of these three cases the epiphyses are anchylosed to the shafts; but the shortness and smallness of all the dimensions, as well as of the head of the femur which falls short of the usual circumference by nearly an inch, indicate that the atrophic condition existed during the period of growth. In each it is observable that the lesser trochanter stands out with remarkable sharpness, the greater trochanter being small, but presenting nothing further remarkable; and in each the length of the neck is about proportionate to that of the length of the bone. The most interesting feature is the openness of the angle of the neck with the shaft, and which in two of the three exceeds that of a fœtal bone. This is also the case in the hydrocephalic skeleton represented in fig. 1.

Fig. 7 represents the stump, with an angle of 142°, taken from a lad who had undergone amputation two years previously (p. 279). It may be inferred that the limb had borne no weight for some time before the operation.

Figs. 8 and 9 represent the stump and upper part of the opposite thigh-bone (the latter measures 18½ inches) from the man (p. 279) who underwent amputation when he was quite young. The stump is small in all dimensions, the head measures 5¼ inches in circumference, that on the other side measuring

6 inches; and the angle is 127°, that on the opposite side being 122°.

Figs. 10 and 11 represent the stump and opposite thigh-bone (the latter measuring 17½ inches) from a man (p. 279) on whom amputation was also performed when he was young. The stump is small, the head of the bone measuring in circumference 5½ inches, that on the other side measuring 6⅛ inches. The angles on the two sides are, however, the same, and are low, being only 115°.

Figs. 12 and 13 represent the stump and opposite thigh-bone from a man, æt. 60, on whom the amputation was performed when he was twenty-four years of age, when, therefore, the growing processes had been completed. Here the bones on the two sides are alike in size and form; the circumference of the head in each is 6 inches, and the angle of the neck with the shaft is 120° in each.

The cause of the openness of the angle in these three conditions, (1) the bedridden state, (2) the paralytic state, and (3) the stump, seems, as stated (p. 280), to be the absence of pressure upon the upper end of the bone from the weight of the body, to which may be added the absence of pressure from muscular action during the period of growth. During development, pressure and growing force combine, in what may be called a "harmonious antagonism," to effect the desired size and form. This is evinced in the various flexures of the spine and of the long bones. In some instances the one preponderates over the other. In tall persons, for instance, the growing force dominates, and the bones are comparatively long and straight. In rickety persons, on the contrary, the reverse is the case, and the bones are too much bent and too short. In the specimens represented in these figures the growing force was weak and the bones are accordingly short and small, but the opposing pressure-influence was reduced in a still greater degree, being indeed almost wanting. Hence the curves in the bones are slight and the necks of the thigh-bones are more nearly on a line with the shafts than natural.

ON THE ORIGIN OF DOUBLE MONSTROSITY. By

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LIKE all the other great teratological problems, though to a higher degree than any other, the subject of double monstrosity has been a fruitful source of dispute, which in this case has been between the supporters of the two great rival theories—that of original duplicity with subsequent fusion, on the one hand, and that of original unity followed by fission, on the other.

That the latter is the correct explanation, appears to me to be rendered more certain by each successive observation which becomes known. Without discussing the *pros* and *cons* of either side, which would be foreign to the intention of this paper, it may be permitted to refer to the most recent evidence in favour of the fission theory.

In a paper on "Birds with Supernumerary Legs,"[1] Professor Cleland has laid down the law, "that in cases of supernumerary legs connected with the sacrum or perineum, the legs developed as the proper legs of the animal belong originally to two different pelvises, being the right limb of a right pelvis, and the left limb of a left pelvis, and that in these circumstances the appended limbs may be two, or one of the two may be suppressed, or there may be a composite limb formed by the undivided blastema for two adjacent limbs of two pelvises." In other words, the smaller pair of limbs are not, as appears to have been taken for granted, fellows, and superadded to the functional, being themselves also a pair, but the true pairs are formed severally of a functional and a non-functional limb.

When the paper above alluded to was written, no recorded human case in all respects bore out the theory put forward, though some did so in a minor degree. Within the last few

[1] *Proc. Phil. Soc.*, Glasgow, 1886; and *Memoirs and Memoranda in Anatomy*, vol. i., 1889. *N.B.*—Professor Cleland informs me that, by a clerical error, the words referring to the sides have been reversed. The quotation above is corrected.

months, however, one has been placed on record which completely bears out Professor Cleland's views.

In the *American Journal of Obstetrics*,[1] Dr Wells gives an account of a female double monster, whose case has attracted some attention in the medical journals. She possesses "a well-formed single body, with normal upper extremities, which below the waist broadens out, having two umbilici, and bifurcating at the pelvis, where there are four lower limbs, all of which spring from the same horizontal and vertical plane. The spinal column divides at the third lumbar vertebra, the two pelves being fused by the junction of their respective ilia. There are two pelvic arches supplying the four limbs, two pubes, two montes Veneris, two perfect sets of external and internal female generative organs, two bladders, two ani, and two lower intestines. The outer limbs on which the woman walks are well developed, though the foot of the right is in a condition of equino-varus. The inner limbs are smaller, atrophied from disuse, and below the knee very rudimentary."

Here, then, as in the cases of the birds, the true pairs are not the functional and the non-functional limbs, but a functional with a non-functional on either side.

Cases such as these, viewed in the light which Professor Cleland has thrown upon them, appear to me to be unexplainable upon any other hypothesis than that of fission. Assuming that this is the true explanation, the object of this paper is to inquire whether recent biological studies give any assistance in the search for the cause of this abnormal division.

At the outset, it may be said that the known facts appear to point to the conclusion that fission, at least in cases of complete or nearly complete duplicity, must take place at an extremely early period, if not at the very earliest. Lists of observed double forms, such as have been given by Rauber,[2] Reichert,[3] and Gerlach,[4] include several which have been met with at very early stages of development, and to these may be added the most recent observation by Burckhardt,[5] of two primitive streaks,

[1] Vol. xxi. p. 1265.

[2] Virchow's *Archiv*, Bd. lxxi. s. 133.

[3] *Arch. für Anat. u. Phys.*, 1864, s. 744.

[4] *Die Entstehungsweise der Doppelmissbildungen*, Stuttgart, 1882.

[5] *Arch. f. Anat. u. Entwick.*, s. 431, 1888.

lying on a single area pellucida, in an egg which had undergone nineteen hours incubation. We may, however, I think, date the time of fission even further back than in any of these cases. Pflüger[1] and Roux[2] have shown that, in *Rana*, the first line of fission divides the embryo into two halves, a right and a left, and that the second, which is excentric, cuts off a larger head segment from a smaller for the tail. That the order in which these lines appear may be variable is admitted by Roux, and this point is confirmed by Rauber's[3] observations on the Axolotl, and those of Goette[4] on Worms; but the important fact is admitted by all these observers, that the early lines of segmentation divide the embryo into different regions. To quote Roux,[5] "the first division of the ovum stands in a strict relation to the chief axis of the body. One line of fission marks out the median plane, another the dorsal and ventral aspects, and another the anterior and posterior portions of the body. With these divisions of the axis go also the corresponding potentialities, dorsal and ventral, oral and aboral, which are differentiated from one another, and deposited on both sides in their proper positions." These observations have been confirmed for other species by Ch. Julin, E. van Beneden, and Nuel.[6]

That occurrences of a parallel nature take place in plants is a strong proof of the law which the foregoing observations, with others yet to be detailed, point to, namely, that the different lines of segmentation cut off from one another cells, or groups of cells, with different potentialities. Dealing with the second or asexual generation of the Fern, Goebel[7] states that the first set of octants form the primitive stem, the primary root, and one or two leaves, also the organ of suction or foot which conveys nutriment from the prothallium to the embryo. The orientation of these is regular:—"The rudiments of the apex of the

[1] *Arch. f. d. ges. Phys.*, Bd. xxxi. s. 311; Bd. xxxii. s. 1; *Virch. u. Hirsch Jahresb.*, i. 91, 1883.

[2] *Ueb. die bestimmung der Hauptrichtungen der Froschembryo.*

[3] *Ber. der naturf. Gesellsch. zu Leipzig*, 1884; *V. u. H. Jahresb.*, i. 77, 1884.

[4] *Abhand. zur Entwick. der Thiere*, Hft. i. s, 7; Hft. ii. s, 56 (*fide* Roux).

[5] *Op. cit.*, p. 44.

[6] Roux, *op. cit.*, p. 6.

[7] *Classif. and Special Morphology of Plants*, Eng. Trans., p. 204.

stem and of the foot lie on the side of the embryo, which is towards the under side of the prothallium, and are therefore turned upwards; the cotyledon and the rudiment of the foot on the side towards the neck of the archegonium, and therefore directed downwards." Again, as in animals, the order in which the septa, constituting the octants, appear is variable, but the parts formed from them are constant. Thus, of the two anterior upper octants one becomes the growing point of the stem, the other undergoes, as a rule, no further differentiation; the two anterior lower octants develop into the first leaf, the cotyledon; the two posterior upper octants form the foot, and one of the two posterior and lower ones forms the root, while the other does not usually develop like the rest."

Roux's[1] most recent work is of further interest in connection with this subject. After the formation of the first line of fission in the ova of *Rana esculenta*, he destroyed one hemisphere with a fine heated needle. Of the ova thus treated, some died, some developed a little further and then also perished, whilst 20 per cent. lived to proceed to more advanced embryological stages. In these the uninjured hemisphere might obviously have developed either into a small but complete embryo, or into a half embryo. The latter, as a matter of fact, was what occurred, and the result, if the first segmentation line had been in the long axis, was to produce lateral hemi-embryos, if in the transverse anterior or posterior hemi-embryos. Similarly, destruction of one of the segments, after four had been formed, led to the production of three-quarter embryos. How far development might have proceeded is an open question, since the oldest artificially killed embryo showed no signs of death, but the observations were carried far enough to establish the facts stated above. From this it follows that the first line of fission separates from one another cells which have different morphological values, since one forms the right the other the left side of the body, or the one the head, the other the tail end, as the case may be. If this be true, then the fission which leads to the formation of duplicity must be something (1) different in its nature, and (2) antecedent to the fission which leads to normal

[1] "Ueb. die künstliche Hervorbringung halberembryonen, u. s. w.," Virchow's *Arch.*, Bd. cxiv. Hft. i. s. 113; and Hft. ii. s. 246.

development. In other words, in cases of duplicity a fission of multiplication precedes the fission of formation. This conclusion would throw back the period of fission to an earlier date than has been fixed by most writers, even the most recent, as for example Born,[1] but I am inclined to believe that it is the most legitimate deduction from the facts detailed.

If fission, then, occurs as the first incident in the development of the double form, it remains to inquire what cause, if any, can be assigned for its occurrence.

Professor Cleland has, in several papers, recently stated his belief that irritation of some kind is this cause. Thus, he says,[2] "every vertebrate animal has, at an early period of its existence, a latent capacity of splitting up indefinitely;" and[3] "double monstrosity consists in the outbreak of proliferation at an unusual period, with consequences dependent on the greater or less perfection of the process, and this outbreak we may fairly impute to irritation." Finally,[4] "over-stimulation, when it occurs soon after impregnation of the ovum, leads to fissiparous division of the germinal mass, resulting in two embryos; at a later period, or carried to a slighter extent, it will cause partial division." In this opinion he agrees with other observers, amongst whom may be mentioned Knoch,[5] who, from his experiments on ova developed in still and running water, the latter affording the greater number of double forms, believed that the agitation was the causative irritation.

Ahlfeld[6] attributes the cleavage to "a faulty relation between zona pellucida and embryo," and his reasons will be found in his well-known work. Kidd[7] formulated the idea which others have held, and which has been criticised by Ahlfeld, that the cause is to be found in a superabundance of formative material. "The formative germ," he says, "is likely to suffer

[1] *Ueb. die Furch. des Eies bei Doppelmissbild, Bresl. ärtzl. zts.*, No. 15, 1887; *V. u. H. Jahresb.*, i. 269, 1887.

[2] *Op. cit.*, p. 11.

[3] "Address to Section of Anatomy and Physiology," *Brit. Med. Jour.*, p. 346, August 18, 1888.

[4] "Teratology, Speculative and Causal," *Mem. and Memo. in Anat.*, p. 128.

[5] Ahlfeld, *ut infra.*

[6] *Missbild. des Menschen*, vol. i. s. 9, Leipzig, 1880.

[7] *Dub. Jour. Med. Sci.*, N.S., vol. xxxiii. p. 464.

from errors of quantity, of quality, and of distribution. The quantity may be in excess and the quality good, giving rise to a double monster, more or less perfect according to the amount of excess; varying from the supernumerary fingers to the parasite and the perfect double monster."

Before proceeding any further in quest of a cause, it may be well to inquire what produces segmentation in the normal ovum. That the power lies in the interior of the ovum, and that division is not influenced by external causes, is the teaching of Roux:—"The impregnated ovum bears within itself all the necessary powers for normal development," and this view is endorsed by Weissmann.[1] In cases of sexual generation at least, then, it must be sought in the action of the male on the female pronucleus. This influence has been compared to the effect of a spark upon gunpowder leading to its explosion. If, however, we follow the view which Weissmann has expounded in his various papers, that "the physiological values of the sperm cell and the ovum are equal, that they are to one another as 1 : 1," the simile and the theory to which it refers cease to be strictly correct. The cause of the division, according to the author just quoted, is the sudden increase of the quantity of the nucleus by copulation with the sperm cell. "The increase of the quantity of the nucleus gives the impulse to division, to which the predisposition previously existed."[2] Excess of nuclear material, nucleoplasm, or to be more correct, "germ-plasma," on this view is the cause of normal division. It may now be asked, turning to abnormal division, whether there is any direction in which such extra amount of germ-plasma may be found, which might permit or favour the occurrence of a fission of multiplication.

There are, I think, several ways in which such excess may be possibly explained.

It is needless to give any account of the well-known facts concerning the extrusion of the polar bodies; it will suffice to allude particularly to Weissmann's observations,[3] now fully confirmed, that in parthenogenetic ova only one such body is extruded, whilst in those which are to be sexually developed,

[1] *Die Continuität des Keimplasma's*, Jena, 1885, p. 17.
[2] *Op. cit.*, p. 98.
[3] *Ueb. die Zahl des Richtungskörper*, Jena, 1887.

two or possibly more are ejected. With the explanation which he gives as to the significance of these two bodies, we are not particularly concerned, yet it may be noted that, even on his own hypothesis, the second consists of true, unaltered germ-plasma, fit for fertilisation and development. In the retention of this, I would suggest, we have one possible cause of the excess of germ-plasma which may lead to the production of duplicity. Whether the nucleus remains single, is fertilised by a single spermatozoon, and then divides into two parts before true segmentation commences, or whether division, complete or partial, takes place with subsequent fertilisation by two spermatozoa, is an open question. In this connection some observations of the Hertwigs[1] are of importance;—"In ova with germinal vesicles, when a spermatozoon enters, there is no change, and no reaction on the part of the protoplasm of the ovum; if the polar spindle has been formed, the heads of the spermatozoa remain unaltered, but a weak protoplasmic streaming occurs. Only after the formation of the first polar body exchange of substance between sperm-cell and germ-plasma takes place, but without the formation of a looped figure (faserige Umbildung)." At the first blush this appears to make against the view just put forward, but it must be noted—first, that a certain effect is possible even in these cases upon the female pronucleus, yet retaining the germ-plasma of the second polar body; and secondly, and this is of great weight, the Hertwigs' own remark (ss. 155, 156), that out of thousands of over-fertilised eggs, only two double larvæ were observed, and their surmise that as no double malformations are known to exist among Echinoderms, which formed the object of their study, these forms may be unfavourable for the production of such monstrosities. One is, I think, inclined to believe that all animals with larval stages would be much less favourable for the production of double monstrosities than those without. Before leaving this part of the subject, it may be mentioned that in plants a process similar to the extrusion of the polar bodies takes place. My colleague, Professor Hillhouse, has been good enough to call my attention to observations of Strasburger[2] on Polyembryony,

[1] *Ueb. den Befruchtungs. u. Theilungsvorgang des thierischen Eies*, s. 147, Jena, 1887.

[2] Goebel, *op. cit.*, p. 401.

which bear a certain resemblance to the occurrences which I have supposed as taking place in the ovum which is to develop towards duplicity, but whether this similarity is real or only apparent I do not feel competent to decide.

Passing to a second possibility, there are indications that the factor at fault may be the spermatozoon. The researches of E. van Beneden and Ch. Julin, as also of Blomfield,[1] seem to show that the spermatozoid gets rid of a portion of its substance (seminal granule) before fecundation takes place. Whether in this way true *reduction* takes place, or whether, as Weissmann[2] suggests, it is effected by the equal division of a cell, each half of which remains as a spermatozoon, we have in either case a means by which an excessive amount of formative material may be retained in the male germ and carried into the female. One observation by Cutter,[3] of spermatozoa with two heads may be mentioned as possibly bearing on this point. Some such occurrence would assist in explaining cases, such as the following, where the male element was obviously the factor producing partial duplication. In this case,[4] the calves affected were borne by seven cows, during the course of a year and a half, the whole herd amounting to forty, the remainder producing normal offspring. Only one of the weaker cows was a primipara, the other six having all previously borne healthy calves. The malformations, which consisted in each case in the existence of a second external ear behind the normal one with a double hyoid bone, commenced after the use of an apparently perfectly healthy bull. When his use was discontinued, these cows bore normal calves.

There yet remains a third possibility, which has been adverted to by several writers, that the excess of material may be due to the entrance into the ovum of two or more spermatozoa. That the normal occurrence is for fertilisation to take place by one spermatozoon, and that the ovum possesses some power by which the entrance of superfluous spermatozoa

[1] For references see M'Kendrick, *Text-Book of Physiology*, vol i. 231; *cf.* also Haddon, *Embryology*, p. 11.

[2] *Ueb. die Zahl des Richtungskörper*, p. 58.

[3] Gaillard's Med. Jour., *Lond. Med. Rev.*, xiii. 291.

[4] "Rost. Veb. eine Reihe von Kalbsmissgeb.," *Sächs. Ber.*, 133,] 1878; *V. u. H. Jahresb.*, i. 605, 1878.

is prevented, has been established by the Hertwigs,[1] yet their researches show that polyspermia may occur, and notably in immature ova. As already noted, this fact has been urged as the cause of duplicity by several writers. Thus Born[2] considers it probable that the entrance of two spermatozoa into the ovum of the frog may lead to double malformations, but not, so far as is known, to twins. Fol,[3] offers a similar suggestion, and states also that "when spermatozoa in excess enter an ovum, they may, under the nourishing influence of the cell body, become centres of attraction and form an amphiaster, *i.e.*, the first figure in the direction of nuclear and cell division. They cannot control the whole cell body and bring it to division, but they exercise a certain power, and do this at the expense of the cell substance." Strasburger has called this "partial parthenogenesis." The reason why the process thus described does not go further is, according to Weissmann, that the supply of germ plasm is insufficient for that purpose. Reverting here to an earlier portion of this paper, it may be asked whether the retention of the whole, or a part of the second polar body, might not supply the lacking material. A similar suggestion as to the result of polyspermia to that of Born has been offered by Marchand[4] and Ziegler.[5] In any of these ways, then, it seems possible that an excess of the true formative material, the germ-plasma, may exist in the oosperm, and lead by its presence to the production of duplicity.

If a sufficient amount be retained and fission is complete, homologous twins results; if the fission be incomplete, then one or other form of true double monster, the amount and site of the connection being due to the amount and direction of the primary lines of fission. Should a smaller amount be present, then, according to the site of its distribution will be the kind of minor duplicity which the fœtus will present.

[1] *Op. cit.*, s. 136; *Bastardbefruchtung.*, s. 45, Jena, 1885; *Lehrbuch der Entwic. Zwte. Aufl.*, s. 35.

[2] Quoted by Weissmann, *Richtungskörper.*, s. 71.

[3] For the second statement Weissmann, *Continuität*, s. 107, is responsible; for the first, Hertwig, *Befruchtungs.*, s. 1.

[4] Ziegler, *General Pathology*, Eng. Trans., p. 24, quoting from *Realencyclopädie d. ges. Heilkunde.*

[5] So states Eimer, *Enstehung der Arten*, s. 201, Jena, 1888, but gives no reference.

Two questions remain for consideration, which can only here be mentioned, since their detailed examination would cause this paper to grow to a size too great. These are, firstly, with regard to the so-called parasites, are such forms due to unequal fission, the smaller half producing the parasite, the larger the autosite, or is the disproportion caused by the blighting effect of the larger and more fortunate twin upon its less successful partner? Secondly, what relation is there between the excess of material which leads to the production of giants, of unilateral congenital hypertrophy of the body, or of a part, such as the face, an extremity, or some of the digits, and that excess of material which it has been suggested in this paper causes the formation of some species of double monstrosity? These are questions which will require consideration on some future occasion.

CONTRIBUTIONS TO THE COMPARATIVE OSTEOLOGY OF ARCTIC AND SUB-ARCTIC WATER-BIRDS. PART III. By R. W. SHUFELDT, M.D., C.M.Z.S.

(*Continued from page 186.*)

HAVING now, in Part I. of this series of memoirs, given a detailed account of *Alca torda*, a representative of the more typical Auks, and in Part II. a similar, though a more comparative, description of another genus, the Murres, which, so far as their osteology seems to indicate, are very nearly related to *Alca*, I am now in a position to enter upon the osteology of other alcine genera, and to make still more complete comparisons among them. In the present Part it is my intention to deal with the skeletons of such other forms of the *Alcidæ* as *Synthliborhamphus*, *Brachyrhamphus*, and *Cepphus*.

Owing to the great rarity of several of the forms in the subfamilies now to be considered, I have been unable to obtain their skeletons, though I made strenuous efforts, in more directions than one, to do so.

It is believed and hoped, however, that the material in the subjoined list will be found sufficient at least to show the leading skeletal characters of the *Phalerinæ*.

Sir Richard Owen presents us with a good figure of the superior view of the skull of *Cepphus grylle*, and an under view of its sternum, in his memoir upon the osteology of the Great Auk, and other authors have figured several of these birds at different times in their works.

Even with the limited material I have before me, the puzzling question now arises,—which form should next be described—which one of these small Guillemots, Auklets, or Murrelets has the greatest number of osteological characters in common with the two genera, *Uria* and *Alca*, described in Parts I. and II.? A glance at one form and we see a sternum, perhaps, that strongly resembles a Murre, but the same skeleton seems, from its other characters, to be inclined Puffin-wards. Another has a pelvis that certainly removes it from the *Alcinæ*; yet again the characters of the skull causes us to hesitate, and re-examine the form we had just laid aside.

The truth is, that we are now upon the very threshold of those almost imperceptible intergradations of structure that we have long known to exist among this and some of the higher groups of birds immediately above them.

Perhaps we cannot do better than present, side by side, the principal characters that the skeletons of two such genera as *Brachyrhamphus* and *Synthliborhamphus* offer us.

Tabulated List of Material.

Specimen and Sex.	Condition, &c.	Complete or Incomplete.	Source.	In whose possession at present.
Synthliborhamphus antiquus.	Dried skull and legs.	Incomplete and broken.	U.S. Exploring Expedition, Oregon.	No. 11,179, Smithsonian Col.
Cepphus columba.	Sternum and pectoral arch.	Complete.	Capt. E. P. Henderson.	No. 17,005, Smithsonian Inst.
Cepphus columba.	Ditto.	Ditto.	Port Althorp, Alaska.	...
Cepphus columba.	Ditto.	Ditto.	June 19, 1880.	No. 17,005, Smithsonian Inst.
Cepphus grylle.	Disarticulated skeleton.	Ditto.	Northumberland Island.	No. 16,776, Smithsonian Inst.
Brachyrhamphus marmoratus.	Alcoholic.	Ditto.	Sitka Bay, T. H. Bean.	No. 81,703, Smithsonian Inst.
Synthliborhamphus antiquus.	Ditto.	Ditto.	Ditto.	No. 81,708, Smithsonian Inst.
Synthliborhamphus antiquus (♂).	Sternum and pectoral arch.	Ditto.	Dr L. Stejneger, at Behring Island.	No. 17,011, Smithsonian Inst. Col.

Observations upon the Skeletons of B. marmoratus *and* S. antiquus.

These Murrelets, upon lateral view of their skulls, have the superior mandible fashioned very much as we found it in *Lomvia*, where the culmen is rounded, and the whole gradually tapers to the tip. The external osseous nares is also elliptical in outline, but proportionately longer. They are without a bony septum narium, and are typical schizorhinal birds, while the meeting of the nasal maxillary, and dentary process of the premaxillary, is like *Uria*. Unfortunately a shot has passed through the ethmoidal region of both the skulls of the Marbled Murrelet, crushing the parts involved. It is evident, however, that the relations of the lacrymal with the nasal and frontal is as in the Razor-bill and Murre. *S. antiquus* shows an ample

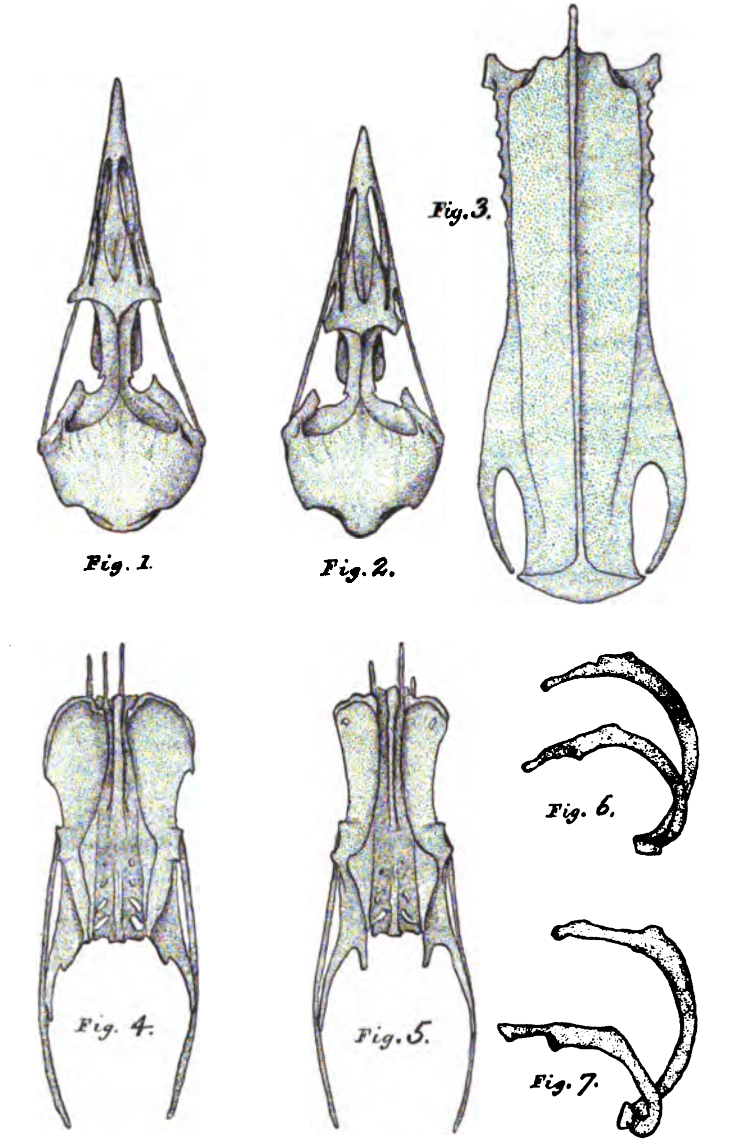


FIG. 1.—The skull of *Brachyrhamphus marmoratus*, viewed from above, mandible removed (specimen 81,703, Smithsonian Collection).
FIG. 2.—The skull of *Synthliborhamphus antiquus*, superior view, mandible removed (specimen 81,708 of the Smithsonian Collection).
FIG. 3.—The sternum of *B. marmoratus*, seen from in front; same specimen as fig. 1.
FIG. 4.—The pelvis from above, *B. marmoratus;* same specimen as fig. 1.
FIG. 5.—The pelvis from above, *S. antiquus;* same specimen as fig. 2.
FIG. 6.—*Furcula* of *S. antiquus*, right side, the bone resting on the plane of the paper; same specimen as in fig. 2.
FIG. 7.—Same view of *furcula* of *B. marmoratus;* same specimen as fig. 1. All these bones life size from nature.

pars plana, with a delicate spine descending from the lacrymal to join its outer margin, but I failed after the most careful examination to detect an os uncinatum, such as I discovered in *A. torda*.

The Murrelets have also large deficiencies in the bony wall of the interorbital septum; the upper and inner part of the posterior orbital wall and the foramen opticum may merge into the former vacuity. The quadrate and quadrato-jugal bar are like as they have been described for the Murres, but a decided change has come about in the position and character of the crotaphyte fossa. Both the birds in hand have this depression confined to the lateral aspect of the skull, with their mesial extremities far apart, and barely to be observed either upon posterior or superior view of the skull. Moreover, this fossa is much shallower in these Murrelets, and its prominent crest-like boundaries, so characteristic of the other Auks described, have mellowed down to such an extent as scarcely to attract our attention.

The skulls of these two genera are compared from superior view in figs. 1 and 2, and the principal points to note are—the form of the superior mandible; the schizorhinal nasal bones and position of the lacrymals; the extreme narrowness of the frontal region between the superior orbital peripheries. This latter is entirely different from what we saw in the Murres, and is due to an absorption of the outer margins of the supraorbital glandular depressions, which absorption gives rise, on either side, to wing-like projections just in front of the fronto-squamosal region. And this is a feature we will find hereafter enjoyed to the highest degree in the Parrot Auks, more especially the true Puffins.

Further, we are to note the subsidence of the crotaphyte fossæ, which allows the vault of the skull in these birds to assume a smooth and rounded superficies, an unusual condition in forms otherwise Auk-like. We are to observe on posterior view of these skulls the receding crotaphyte fossæ; the great prominence of the supraoccipital protuberance, especially in the Black-throated Murrelet (fig. 2); in both of these specimens this is pierced on either side by the occipital foramina, but other skulls of these genera may have them missing. These

Murrelets show also a convex elevation on either side of the supraoccipital prominence between it and either of the lateral auricular fossæ.

The plane of the foramen magnum making an angle with the basi cranii of about 45°, we can also see this aperture on direct posterior view; and below it the form of the hinder aspects of the quadrates are as they appear in the Murres.

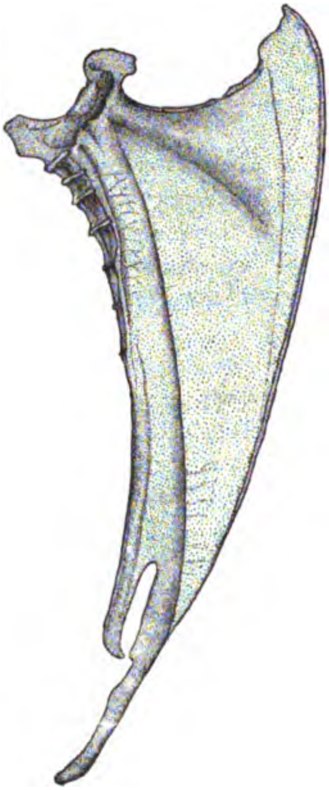


FIG. 8.—Right lateral view of the sternum of *Cepphus columba*; life size, from specimen 3294 of the Smithsonian Collection.

Turning the skull so as to give us a direct under view, we note that the palatal structure is arranged precisely as in the Murres, with a few slight modifications. The maxillo-palatines are elliptical, not spongy, and approach each other very closely in the median line. The *vomer* is united with the palatines as

in the Murres, but we notice that there is a disposition for it to develop a spine on its anterior extremity, as seen in the *Laridæ.* It bears the same relations to the surrounding bones as in *Uria* and *Alca.*

The palatines and pterygoids are also fashioned upon the same plan; the postero-external angles of the former are rounded. No evidences of basipterygoid processes are observed. A lip of bone overhangs the double opening of the Eustachian tubes. The basi-temporal region is broad transversely, and its general area ample; the foramen magnum is subcircular, and the condyle of the occiput is hemispherical, sessile, and small. Finally, it must be noted that the antero-superior end of the ethmoid is transversely divided beneath the cranio-facial hinge, as in the Murres and Razor-bill, and that the rostrum is long and slender, being produced far to the front, between the limbs of the vomer, as a spiculaform process.

Brachyrhamphus has a *mandible* that exhibits the characters of this bone in the Murrelets very well. In it the ramal sides anteriorly are narrow from above downwards, and longitudinally furrowed between the forks of the dentary to within a short distance from the tip. Behind the sides are deeper, and the coranoid process is fairly developed. Both upper and lower borders of each ramus are rounded, while anteriorly the symphysis is short, and scooped out in the median line above.

The elliptical foramen is still seen, and of considerable size, in the surangular, but in these birds the splenial may fail to quite close the true ramal vacuity. The inner articular processes are roundly expanded at their tips, and they are directed somewhat backwards. At each angle we observe a sharp recurved process, the tips of each rising slightly above the level of the articular facets. After a careful examination of the mandible, I believe it to be a non-pneumatic bone in these two genera.

Murrelets have the *hyoid arches* constructed as described for *Uria,* the glosso-hyal is entirely in cartilage; the basibranchials anchylose together, and they seem to differ from the Murres in having the bar which connects the cerato-hyals, ossify.

Though agreeing in all essential particulars with *Uria,* the

vertebral column of both these genera under consideration have one less vertebra in the cervical region. It will be remembered that the first pair of free ribs occur in *Alca* and *Uria* on the fourteenth vertebra, while here in the Murrelets these free riblets are suspended from the thirteenth vertebra. After that, the arrangement for both *Brachyrhamphus* and *Synthliborhampus* is that, their *fourteenth vertebræ* also have a long pair of free ribs, that support unciform appendages (as in the fifteenth of *Uria*). Then occur seven vertebræ in the dorsal region of either of these Murrelets, with their long hypapophysial processes, {the leading ones being bicornuted, and all with the parallelogramic neural spines; while five or six of the ultimate ones have the opisthocœlian joints among the centra. These seven vertebræ all have long, sweeping, vertebral ribs, that connect with the sternum through hæmapophyses of a character similar to those in other Auks. There is also another pair of vertebral ribs which articulate with the pelvis, but whose costal ribs do not reach the sternum. All these ribs, but the eighth or last pair, have long epipleural appendages, which articulate with their posterior borders, except in the first pair, where they seem to be anchylosed to the rib.

Figs. 4 and 5 compose the superior aspects of the pelves of these two Murrelets. As well as I can ascertain, after careful count, each one seems to have thirteen vertebræ anchylosed in its sacrum, the five anterior ones throwing out apophysial abutments against the under walls of the ilia; next come three with aborted processes; then five more, which again have projecting apophyses. Between these last occur the double row of foramina seen on the view presented in the figures.

It will be noticed that the pelvis is becoming shorter and wider, as evidenced in the form it assumes in the Marbled Murrelet. On the other hand, it retains the general appearance in the Black-throated Murrelet, as presented by *Uria, Plautus,* and *Alca.*

In both, the post-pubis is long and gently curved throughout, a large elliptical ischiac foramen is present; the obturator foramen opens into the obturator space, but the notch between the ischium and ilium on the posterior border has nearly disappeared in *Brachyrhamphus*, while in *Synthliborhamphus* it agrees more with *Alca* and others.

In *S. antiquus* there are *nine* free vertebræ in its tail, with a long, narrow pygostyle. A few of the ultimate ones have small bifid chevron bones, and the transverse processes of the series are nearly of an equal length, except the last two, where they are nearly aborted, quite so in the last one. Otherwise they agree as found in the class generally. We find but *seven*

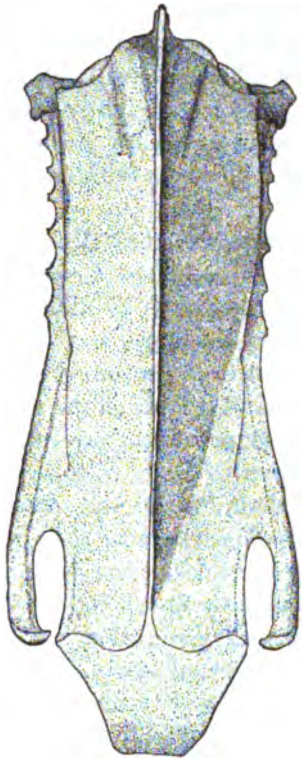


FIG. 9.—Inferior aspect of the sternum of *Cepphus columba*; life size, from specimen 3294, Smithsonian Collection.

free caudal vertebræ in *B. marmoratus*, and the chevron bones are not bifid. Moreover, the pygostyle is comparatively much shorter and broader. The transverse processes of these vertebræ are also wider than they are in the skeleton of the tail of the Black-throated Murrelet.

I have compared the clavicular arches of these two birds in figs. 6 and 7; from them it will be seen that all the characters

of an Auk's furcula is present in each. The long head of the clavicle is there, with its raised outside mid-facet for the head of the coracoid. On front view both have the characteristic U-shaped pattern, the limbs being curved backwards, and support a small hypocleidium where they unite below. In neither genera does the posterior end of a clavicle meet the scapular process or the scapula behind.

This latter bone is long, narrow, curved, and posteriorly truncate; its head is broad transversely, compressed from above downwards mesially, it projects slightly over the scapular process of the coracoid, while externally it supplies, by an elliptical concave facet, the glenoid cavity with one-third of its articular surface.

Essentially, the coracoids of these Murrelets agree, except in point of size, with the coracoid of *Uria*. In *B. marmoratus*, however, the scapular process is so narrow from above downwards, that the foramen which pierces it in other Auks is here missing, it being present in *S. antiquus*. The coracoidal heads hook far forwards to meet the facet on the outer side of the clavicular head, and the very prominent process, straight in *B. marmoratus*, crooked upwards in *S. antiquus*, at the lower and outer margin of the shaft, lend to the coracoid of these birds a distinctive character enjoyed only by the typical *Alcidæ*.

A glance at fig. 3 is sufficient to assure us that these Murrelets have a true Auk's sternum, being long and narrow, deeply 1-notched; wedge-shaped manubrium; deep carina gradually sloping away to the xiphoidal end of the body, and finally, in common with the pectoral arch, non-pneumatic.

There are seven facets on each costal border, and it is to be observed that the pectoral line of the ventral aspect has left the edge of this latter, and moved towards the median line somewhat. A side view of the sternum in *S. antiquus* would appear very like that bone in *A. torda*. In *B. marmoratus* it has the same general appearance; but we should note that these externo-posterior xiphoidal processes are gently curved outwards, after the fashion of the Parrot Auks and *Cepphus grylle*, though not to such an extent.

The *pectoral* and *pelvic limbs* of the Murrelets can be briefly disposed of in a few words, as they agree in all important par-

ticulars with the bones of the appendicular skeleton of *Uria* and *A. torda;* and these have been described in detail in previous paragraphs. In both genera the bones of the limbs are non-pneumatic, and with contracted medullary cavities. The humerus has the characteristic flattened shaft, and in the closed

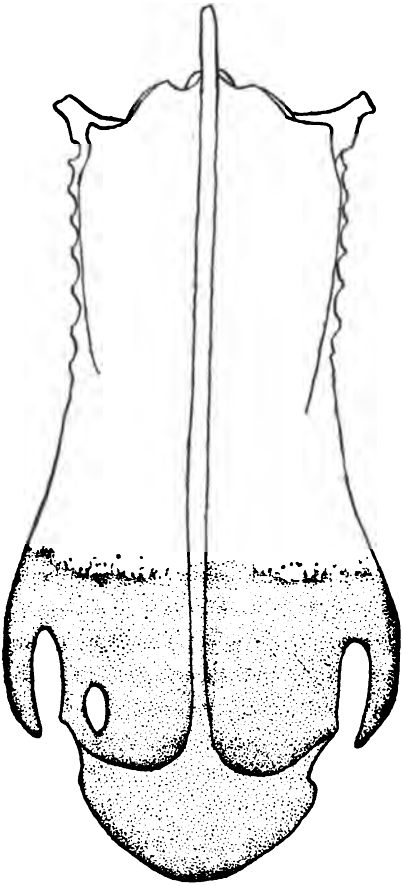


FIG. 10.—Outline of inferior aspect of sternum of *Lomvia cirrhata* (specimen 13,656, Smithsonian Collection); life size, by the author.

wing is one-fourth longer than the bones of the antibrachium which lay beside it.

Radius and ulna have also flattened shafts, with rounded borders in the interosseous space, and sharpened ones on the opposite sides. There are three sesamoids about the elbow, as

in *Fratercula,* figured beyond. The skeleton of the hand agrees with *Uria;* the pollex has but one long phalanx, and no claw. This is true also of the last phalanx of the index digit. The composition of the carpus is the same.

In the *pelvic limb* the femur is like it, as in *Alca torda,* except, of course, in point of size. A small patella is present, surmounting the apex of the cnemial process of tibia, as in *Uria* and the Puffins. The tibia has a peculiar twisted appearance in the Marbled Murrelet; it is, as it were, for its proximal half turned a little towards the fibula side, carrying the latter with it.

This makes it appear as though the lower half of the fibula was inclined to get on the front of the bone, while actually the small ectocnemial ridge of the tibia is turned considerably outwards, and the large procnemial one looks straight to the front above, but it too is turned slightly outwards below, subsiding abruptly into a line on the shaft; that in *A. torda,* for instance, is on the internal aspect. Otherwise the cnemial process is to all intents like the Auk just mentioned.

The distal end of tibia agrees with *Uria* and other Auks, as does the skeleton of metatarsus and pes in all important points.

B. marmoratus, in the condition of its tibio-tarsus just alluded to, differs with *S. antiquus,* in which latter form the bones of the leg agree with *Alca, Plautus,* and *Uria.* Now, as I have said in a former paragraph that the tarso-metatarsus of *B. marmoratus* agrees in all important points with *Uria,* this does not apply to certain details, but rather to its general form, proportionate length and calibre, and its grooved hypotarsus, it remains for me to point out certain details of structure, and compare them with the Black-throated Murrelet and others. Omitting the toes, which practically are much alike in these two genera, so far as proportionate lengths are concerned, I will present the lengths of the long bones of this extremity, so as to call attention to their variance, with special reference to the tarso-metatarsus, as I will have something to say about the difference this bone has in these genera immediately afterwards. These measurements are in centimetres and fractions.

	Femur.	Tibia.	Fibula.	Tarso-metatarsus.
S. antiquus, . .	2·4	4·6	2·7	1·7
B. marmoratus, . .	2·6	4·9	3·2	2·8

In *B. marmoratus*, as in *Uria*, a transverse section made at mid-shaft of the tarso-metatarsus, the figure would be a parallelogram, and the faces of the bone are flat, the anterior and posterior ones being wider than the lateral ones. The Murrelet possesses that which the Murre does not, however, and that is a

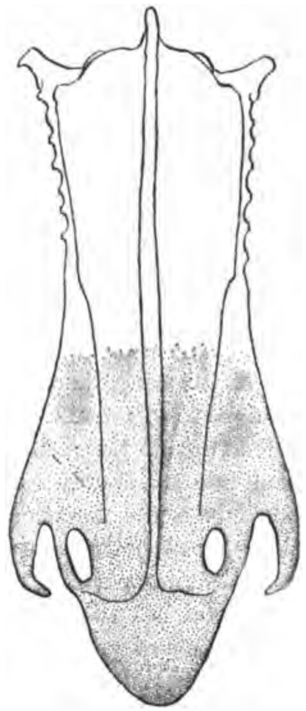


FIG. 11.—Outline of inferior aspect of sternum of *Fratercula corniculata* (specimen 13,652, Smithsonian Collection); life size, by the author.

rudimentary first metatarsal anchylosed to the shaft about in the same position, and of a similar form, as we find it in *Hæmatopus*.

In *S. antiquus*, a bird with a tibia, as in typical Auks, has a metatarsus constructed very much like that bone as we find it in *Urinator*, *i.e.*, compressed from side to side, grooved down

the back, and less so down the front, for the lodgment of tendons. The trachleæ are also compressed, like the shaft, with the inside one thrown to the rear, and curved inwards. In other words, the tarso-metatarsus of *S. antiquus* has the proximal extremity constructed as in true Auks, with a slightly more prominent hypotarsus, while all the lower part of the bone is closely fashioned after the Loons, and it lacks the anchylosed rudimentary first metatarsal seen in *B. marmoratus.* The proximal ends of the phalanges of the toes are also modelled to accommodate themselves to this urinatorine modification in the foot of this Murrelet.

Remarks upon the Sternum and Pectoral Arch of Cepphus columba.

To represent the osteology of this species, my material offers me but the three sterna with the attached hæmapophyses, and the three corresponding pectoral arches of the Pigeon Guillemots, collected by Captain E. P. Herendeen at Port Althorp, Alaska, on the 19th of June 1880. These bones, however, present several points of interest, illustrating in particular a fact that we have already alluded to; and that is, the inconstant character of certain structures in the skeleton of Birds. These arches and sterna are all non-pneumatic, and the hæmapophyses go to show that the skeleton of the thoracic parietes of *Cepphus columba* agrees in its general outlines with other Auks and Guillemots. As will be seen from the figures illustrating this and other Parts, the sternum has the common pattern or style of the bone in the *Alcinæ* generally.

In all three of them the mesial extremities of the coracoidal grooves are separated by the base of the manubrium, while the articulatory surface is continuous into the pits at their outer ends. Two of these bones have seven articular facets on each costal border, the remaining sternum having but six, and in it, probably, the hæmapophyses of both pairs of sacral ribs failed to connect. All of these sterna are 1-notched, the lateral processes thus produced having a slight tendency to flare out or point a little outwards as well as backwards; the middle xiphoidal portion being extended more posteriorly than in other

Guillemots. This part is perforated by two foramina in one of the specimens, near the margin on the right-hand side.

Now, it almost seems that this notching of the sterna in birds progresses something like this:—take *Plautus impennis*, for instance; it represents the simplest form of the body of the bone that could well be—long and narrow, and a round xiphoidal extremity often without notch or foramen. The next step is a foramen—but what the original necessity or cause for the appearance of this was, I am not now prepared to say—but an elliptical foramen makes its appearance in a sternum of the form of the bone in *Plautus*, and even as we now know in the sterna of the young of that bird, between the hinder end of the muscular line and the thickened outside border of the body of the bone, a little anterior to the semilunar area found at the extreme posterior termination of such sterna. A bone in this stage I now hold in my hand (No. 16,986, Smithsonian Coll.). It has but the one foramen described; the opposite side being entire, as in Owen's figure of *Plautus*. This specimen belonged to a *Uria troile*, and I am satisfied that, should we examine a sufficient number of the sterna of this last-named species, we would eventually come across one in which the xiphoidal end of the sternum would be entire, *i.e.*, without either foramina or notches.

Next, we can easily see why two such foramina might present themselves, and further the necessity for the modification still in operation, see how such foramina might increase sufficiently in size so as to cut through the bone at the weakest point, *i.e.*, the posterior margin, being guided in that direction by the muscular line and the thickened outside border. Then we have sterna like those in *Lomvia* and Brünnich's Guillemot respectively, the processes formed still being parallel to the long axis of the bone, or to the keel, as for that matter. Now comes, from perhaps the same cause or necessity, or the operation of an additional necessity, a tendency for these processes to flange outwards, and a general widening of this end of the bone in consequence. The first stages of this step is seen in fig. 9, after which the sternum seems to gain a little in breadth generally, or may be, too, lose a little in length, but more probably the former. This gives rise to the necessity for additional foramina

in the broadened xiphoidal extremity, and we see the result in the sterna presented in figs. 10, 11, and 17 respectively. Such forms once brought about, and laws ever in operation still acting, as the influence of heredity for instance, it makes but slight demands upon our imagination to see such a sternum eventually assume the form it has in a Turkey. Nor would it be difficult for us to imagine how from different causes coming into operation, hastening matters here, checking matters there, that another series might arise, terminating eventually in such a sternum as is possessed by a Tinamou, *T. robustus*, for instance.

Fig. 38 shows the inside view of the pectoral arch of one of these specimens of *Cepphus columba*, and no doubt will give a better idea of its form than anything I might attempt by way

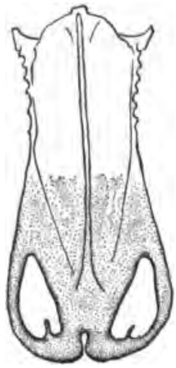


FIG. 12.—Outline of inferior aspect of sternum of *Simorhynchus pusillus* (specimen 12,664, Smithsonian Collection); life size, by the author.

of description. There are a few points, though well worthy of our notice, that it does not show. Among these is the fact that the posterior end of the head of either clavicle may reach the head of the scapula in some cases, as it does in specimen No. 3294 of this set. Attention is called to the additional fact that these clavicular heads are not as long, comparatively speaking, as they are even in the smaller Auks and Guillemots.

There is a tendency, too, for their ends to become thickened or clubbed. A variation is seen also of some little importance in the coracoid, and this series of Guillemots, all of the same species, shows it very well. It refers to the lower part of the

scapular process of this bone and its perforating foramen. In one specimen this process is carried a considerable distance down the shaft, and, in consequence, the foramen is present and perforates it. In another specimen the scapular process is so short that the foramen only creates a notch at its lower margin; finally, in the third specimen the process is so narrow from above downwards that, not reaching the point opposite where the nerve that passes through this foramen must always be, it is not perforated at all, nor even notched.

It will be noticed that the blade of the scapula is long and very narrow in these birds, its truncate posterior extremity being slightly dilated at the apex.

The Skeleton of Cepphus grylle (*the Black Guillemot*).

Owing to the existence of so many large apertures through the skull of this Guillemot, it has a very light and open appearance on lateral view. In general composition it resembles the skull of some of the Murrelets, with several interesting modifications and characters of its own.

On side view, we find a long tapering superior mandible, with broadly rounded and straight culmen. The narial aperture is also very open, and reaches two-thirds the distance towards the apex from the anterior margin of the nasal on either side. Like all other Auks, *Cepphus grylle* is a schizorhinal bird, the slits in the nasals being carried up to near the anterior margins of the orbital peripheries.

The dentary processes of the premaxillary are narrow, thin, horizontal plates of bone; the anterior part of each palatine that extend them backwards is even still narrower and more slender.

Each lacrymal is a very delicate bone, and seems to be attached simply to the upper and outer angle of the nasal—a fine slit dividing the bones below the point of attachment. The spiculaform process that the lacrymal sends downwards barely meets the outer edge of the ethmoidal wing of the same side, and I fail to find an os uncinatum present in this bird. These ethmoidal wings are very thin and feeble productions, that do not reach the vault above nor very effectually divide the orbit

from the rhinal chamber otherwise. Were it not for a narrow lamina of bone that spans the interorbital space, this Guillemot would rival the Cormorant in its meagre bony partition separating the orbital cavities.

A large portion of the antero-superior wall of the brain-case lacks an osseous wall here, and the common vacuity thus created is united with the open area along the track of the olfactory nerves.

The structure of the ethmoid agrees essentially with that bone as described for the Murrelets. It stands out prominently

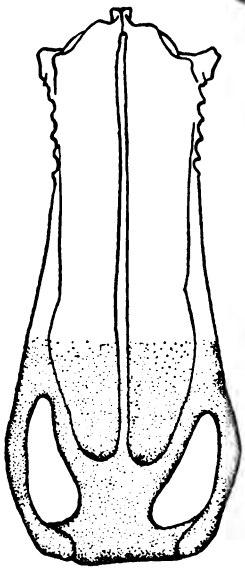


FIG. 13.—*Cyclorrhynchus psittaculus*; outline of inferior aspect of sternum; life size (specimen 13,649, Smithsonian Collection).

here, owing to the absorption of the interorbital septum and the delicate formation of many of the bones in its neighbourhood.

So far as our investigation has carried us, there seems to be little or no change in the shape or character of the quadrate. In this Guillemot the facets on its foot, the general form of its orbital process, its head, and, finally, the way it receives the quadrato-jugal bar, all agree very well, even with *Alca torda*. *Cepphus grylle* has its crotaphyte fossæ more distinctly impressed upon each side of its skull than we found them either in *S. antiquus*

or *B. marmoratus*, and their inner extremities approach each other nearer in the median line behind.

In this latter locality they seem to have been checked by the presence of the dome-like supraoccipital prominence, which stands right between them. This shows nicely in Professor Owen's figure of the superior aspect of this Guillemot's skull in his Memoir upon the Osteology of *Plautus impennis*.

In other particulars this upper view of the skull of the Black Guillemot reminds us very much of the same view of any of the skulls of the Murrelets. The same narrowness obtains between the superior orbital margins, but in this particular specimen it does not create with an equal distinctness those lateral wings so prominent in the Puffins, and which were described also for the Murrelets.

This bird has a comparatively large brain cavity, the outside of the cranium above being smooth and broad transversely. Within, the pituitary fossa has a solid posterior wall, the carotid apertures being double at the bottom of the pit. Quite massive, too, are the bony prominences of the middle ear upon the interno-lateral cranial wall, while a crest-like tentorium divides the fossæ of the big and little brain.

Upon the posterior aspect we see a large foramen magnum, cordate in outline, with the apex upwards.

The condyle is very small, sessile, and of a hemispheroidal form. The plane of the foramen makes an angle of about 45°, with the basis cranii, or rather with the latter plane, posteriorly reversed.

An under view of the skull of *Cepphus grylle* has the general arrangement of parts and the palatal structure of the foregoing descriptions of other Murres and Auks. There are, however, a few special points to be noticed in this bird, and first among these stands the form of the *vomer*.

This bone is forked behind, as usual, for the long spine-like anterior process of the slender rostrum and the ascending processes of the palatines. Above it is longitudinally grooved, and below carinated, and the margins thus formed are produced anteriorly into a pointed spiculaform process, such as we find among the *Laridæ*, and here rides in the groove of the vomer.

The maxillo-palatines are flat, laminated, elliptical discs, placed

as in the Murrelets, though reaching further backwards. Posteriorly, the palatine bodies are truncate from the heads forwards. The horizontal plates of the maxillaries are each perforated by a single round foramen, as in many of the Puffins, but so far as my material will permit to say, absent in the true Auks. Feebly developed "prickles" are found at the sites of the basipterygoid processes on the sphenoid, but corresponding spiculæ, in this specimen at least, are not seen upon the pterygoids.

The *mandible* of *Cepphus grylle* is formed very much as we found it in the Murrelets. At the side, the true ramal vacuity is closed by the splenial and the broad lower fork of the

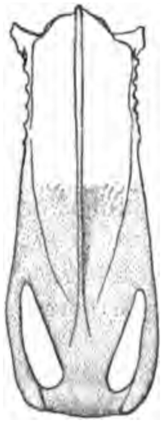


FIG. 14.—*Simorhynchus pygmæus*; outline of inferior aspect of sternum; life size (specimen 17,018, Smithsonian Collection).

dentary. Upon the inner aspect the splenial element is quite distinct in the adult bird, and anteriorly it spans over quite a fossa that is found in this locality. The base of this fossa posteriorly is formed by the surangular, and in this Guillemot is pierced by two small foramina, one in front of the other. differing in this respect from the Murrelets and *Uria*. Very weak coronoid processes are seen at their usual places upon the superior ramal borders, and the articular ends are compressed from above downwards to a degree not noticeable in many of the other Auks.

Recurved processes are found at the mandibular angles, curving upwards, forwards, and outwards; while the inner pro-

cesses are clubbed at their extremities, and are directed upwards, backwards, and inwards. An excavation is found behind, between these two processes, which is bounded by a raised line extending from the base of the former to the apex of the latter, curving forwards in its course on the under side of the articular end.

Cepphus grylle has its hyoid arches constructed as they are in other Auks and Guillemots described above, with slight specific variations unworthy of special mention.

There are thirteen vertebræ in the skeleton of the neck of the Black Guillemot before we arrive at that one which bears a diminutive pair of free ribs, which occur on the fourteenth. The fifteenth vertebra also has a pair of free ribs, but as in other Auks, they are longer, with epipleural appendages attached to them. Returning to the series without ribs, we find the atlas to be scarcely distinguishable from the bone as it occurs in *S. antiquus* or similar forms. The upper part of its cup is circularly notched to admit the tip of the odontoid process of the axis. This latter segment also agrees very closely with the axis of forms described in previous paragraphs. Indeed, were it not for its size, it would be difficult to pick out a single point wherein it differs from the axis of *Alca torda*. It is about half the size of the second vertebra in that Auk.

The third and fourth vertebra have both neural spines and hypapohyses, as well as the lateral canals, but they are recognisable principally for their more solid appearance, due to the pre- and postzygapophyses being united by continuous osseous lamina, being simply perforated on either side by a small foramen, of an equal size in each vertebra, in the specimen in hand.

The fifth vertebra also has a small neural spine and long hypapophysial crest. In it the parapophysial processes commence, and pleurapophysis inclosing the lateral canals, and these continue till they result in the aforesaid free ribs of the fourteenth vertebra. Precisely as we found it in the Razor-bill, this Guillemot has its carotid canal on the under side of the sixth, seventh, eighth, and ninth vertebræ. It is an open channel in all four, and the tenth vertebra has a large hypapophysis in its place. This is continued through the succeed-

ing three vertebræ, it becomes forked in the fourteenth and tricornuted in the fifteenth, which latter again assumes a neural spine.

In general characters and number (7) the vertebræ of the dorsal region of the Black Guillemot agree with the same series in *Alca*. They have the opisthocœlian articulation, the hypapophyses dipping far into the thoracic cavity, gradually diminishing in size as we proceed backwards; and, finally, they are non-pneumatic like the other vertebræ of the column of both these genera.

Seven ribs connect with the sternum by costal ribs, another pair articulate with the sacrum, but whose hæmapophyses do

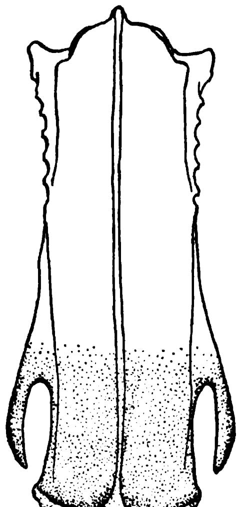


FIG. 15.—Outline of sternum of *Synthliborhamphus antiquus*, inferior aspect (specimen 17,011, Smithsonian Collection); life size, by the author.

not reach the costal borders. All have freely articulated "epipleural appendages" except the last-mentioned pair, where they are absent. These appendages are long, and the ribs, both vertebral and costal, are gradually produced far backwards in gentle curves, as we find them among the *Alcidæ* generally.

Cepphus grylle evidently approaches the Puffins in the form

of its *pelvis;* the most superficial examination of this bone, and its comparison with the pelvis of Brünnich's Guillemot, and then with such a form as *Lunda cirrata,* would surely convince us of this. It has not the long narrow form of the true Auks, but exhibits nearly all the characters as seen in the pelvis of the typical *Fraterculinæ.* Its ilio-neural canals are open grooves; its post-acetabular area is about equal to the pre-acetabular. The sides to the rear of the cotyloid cavities are more spread out, and the whole posterior part generally broader.

The double row of interapophysial foramina of the sacrum are present, and the notches on the posterior border between the ilium and ischium are well marked.

Viewed laterally, we note that a large elliptical ischial foramen is present, as in *Uria* and others; the obturator foramen opens by its entire hinder half into the obturator space, thus creating one great elongated opening between the lower margin of the ischium and the upper margin of the post-pubic element. The ischium is produced far behind as a long attenuated process. No sign of a pro-pubis exists; and either ilium in front of the cotyloid cavity is generally concave to its very anterior border, which latter is rounded, and shows a faint emargination.

A ventral view of the pelvis reveals to us the fact that there are but twelve vertebræ included in the sacrum; the anterior five of these throw out their apophysial abutments against the nether walls of the ilia. Next, in the basin proper of the pelvis, come three, in which the pleurapophysial processes have aborted, while their diapophyses form a part of the dorsal vault of the sacrum. The ultimate four vertebræ have these apophysial elements coössified, and extended between the inner margins of the latter halves of the ilia.

Air does not gain access to the bones comprising the pelvis of this Guillemot, and there is no evidence of pneumatic foramina at their usual sites.

Nine free vertebræ are found in the tail of *Cepphus grylle,* and a pygostyle, which probably includes about three more. The diapophyses of the third, fourth, and eighth are obviously shorter than in the others. In the ninth they are entirely suppressed, and in all they are somewhat deflected. The pygostyle and the next two vertebræ beyond have the chevron bones

anchylosed to them. A small neural canal passes through the entire series. As compared with *Uria*, the pygostyle is very much shorter, having more the appearance of that bone, as found in some of the higher groups of birds, than it has to any of the true Auks.

So much has already been said about the *sternum* of this Guillemot in some of the comparisons made above with other *Alcinæ*, that it may be disposed of here in a few words. In the present specimen the inner ends of the coracoidal grooves do not meet at the manubrial base, being separated from each other by an interval fully equal to the one we found in *C. columba*. Seven facets are found in each costal border, but experience teaches that specimens may come to hand where there are found to be but six, or, as I have observed it in other water birds, six on one side and seven on the other. As in other Auks, the carinal angle of the Black Guillemot is produced as a prominence in front of the keel, like *C. columba*. The hinder half of the bone is more dilated than is the case with the sternum of a typical Auk; the lateral xiphoidal processes stand out, and foramina usually occur over their inner borders; finally, the mid-xiphoidal part is rounded behind, and rather more produced than in such a form as *Lomvia troile*, for instance. Agreeing with other *Alcinæ*, the sternum of *C. grylle*, though very thin and light, is entirely non-pneumatic.

Passing to the *pectoral arch*, we find that, although agreeing in all its principal points with this part of the skeleton, as described for other Guillemots, its clavicular heads are very noticeably shorter, their posterior ends more dilated or laterally compressed, and the facets for the coracoidal heads more prominent.

The U of this arch is more contracted, and the hypocleidium rather smaller.

The coracoid and scapula agree with these bones, as described for *C. columba*. In the present specimen the foramen exists in the scapular process of the former element; but I believe a series of skeletons of this Guillemot would show that it might be absent in some specimens, as we found it in the Pigeon Guillemot. When articulated, as in life, the head of a clavicle fails to meet posteriorly, either the scapula or the scapular

process of the coracoid; the existing interval, however, is very slight.

Nothing could show more perfectly the extreme gentleness with which some of the characters of the skeletons of several of these forms diverge from each other, or from some ideal type which we have endeavoured to fix in our minds, than the pectoral limb of *C. grylle.* If we allow the humerus of *Alca* to be our ideal of this bone in an Auk, then the present one, by almost an insensible and gradual departure, has now nearly the form it assumes among the Puffins.

The palmar aspect of the proximal end is more rounded, and the radial crest more bent in that direction, while the shaft of the bone can no longer be said to be flat, but rather subcylindrical, throughout its continuity, until we arrive at the distal end, where it is enlarged to support the articular facets. Even here an almost indescribable change has come about; the bones seem to be alike, yet they are unlike. Perhaps it may be due to the rounding of the humeral shaft in *Cepphus,* and, as it were, the barest imaginable fulness had passed into its distal extremity, the whole bone being on the very verge of losing all its flat appearance—a condition which pertains to, and that at once impresses the ornithotomist when he picks up the humerus of *Alca torda.* In the Black Guillemot the ectocondyloid tubercle of this bone of the brachium is so reduced as to be scarcely noticeable. We will find that this character becomes quite prominent in some of the forms to be hereinafter treated. I regret to say that the sesamoids that occur at the elbow of most Auks and Guillemots, if possessed by the present bird, have been lost, and I am in consequence unable to state their number or anything about them.

All that I said above in regard to the humerus applies with equal force to the bones of the anti-brachium of the form in hand. Their shafts are here nearly devoid of all flatness, and they have assumed a style enjoyed, to a greater or less extent, by the great majority of water birds, and one which, if the bones were examined apart from the remainder of the skeleton, might not strike us as belonging to an Auk—at all events, we would not be as positive in our diagnosis of them as we would be if we had the ulna and radius of a Razor-bill in our hands.

No special comment is called for in the consideration of the bones of the hand in *Cepphus grylle;* they all agree very closely with the corresponding bones in the manus of the Murrelets, both in number and general form. Although it apparently has been lost, a careful examination of the highly magnified distal end of pollex phalanx inclines me to believe that these birds have another minute joint added there; and this belief is

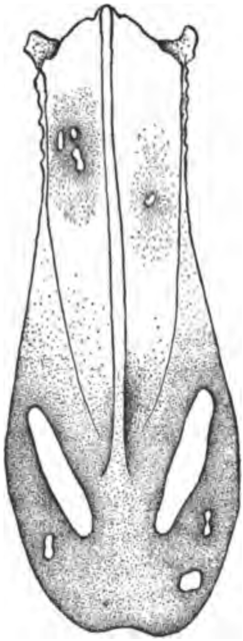


FIG. 16.—Outline of sternum of *Simorhynchus cristatellus*, inferior aspect (specimen 17,028, Smithsonian Collection); life size, by the author.

strengthened by the fact that such a structure is present in the Puffins.

As taken in centimetres and their fractions, the bones of the pectoral limb of *Cepphus grylle* measure respectively—the humerus, 6·0 cms. long; the ulna, 5·0; the radius, 4·8; the carpo-metacarpus, 3·4; pollex phalanx, 1·4; proximal joint of index, 1·4—lowermost one, 1·6; and the small joint of the middle finger, 0·7. The limb is non-pneumatic.

In the *femur* of the pelvic extremity we are to note the

absence of the trochanterian ridge at the summit of the bone, although it becomes immediately quite prominent on the line below. The cylindrical shaft is but slightly bent, so as to be convex forwards, principally just above the lower third.

When the femur is held vertically, the outer condyle is the lower; it is also the larger, and has the inner ridge of the fibular cleft prominently produced, forming quite a character-

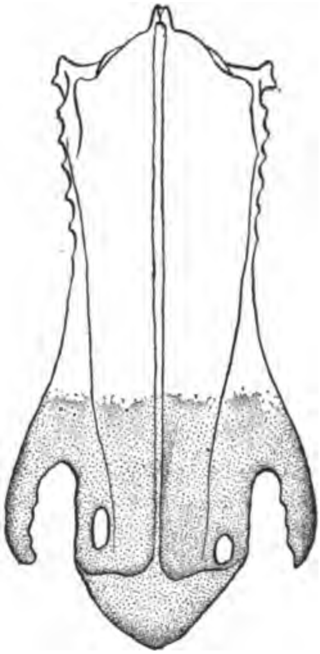


FIG. 17.—Outline of sternum of *Cepphus grylle*, inferior aspect (specimen 16,776, Smithsonian Collection); life size.

istic feature of the bone in this bird. As in the case of the excavation in the head for the round ligament, the popliteal depression in the femur of this Guillemot is almost obliterated.

A patella is present, occupying the same position as it does in *Uria* at the apex of the cnemial crest. Indeed, the leg bones agree in all essential characters with the leg bones of the Murre, the tibial shaft being straight and subcylindrical between the fibular ridge and where the bone begins to enlarge below to support the condyles. The lower end of the fibula in this

specimen does not anchylose with the shaft of the tibia, and the upper third of this bone is much compressed from side to side.

A section made perpendicular to the shaft of the tarso-metatarsus at its middle would be square in outline. In this it differs from *Alca*, where the anterior and posterior faces are wider than the lateral ones.

Proximal end of the bone agrees with the Murres as a whole, but *Cepphus grylle* has a more prominent hypotarsus, which shows one vertical tubular perforation in addition to being grooved at its back.

The distal trochleæ are comparatively large, but arranged as described for *Uria*.

As in *Brachyrhamphus*, an anchylosed, laminated, and diminutive process occupies the site of the metatarsal accessories.

The joints of the toes are of much larger calibre and generally stouter than we find them in the Murrelets, though, of course, in their number and method of articulation, they agree with the *Alcinæ* generally, even the generic variations being very slight in most of these birds. Measuring these bones as we did in the case of the pectoral limb, we find the femur to be 3·6 cms. long; the tibia, 6·3; the fibula, 4·0; the tarso-metatarsus, 3·2; the joints of the outside toe, 1·0, 0·75, 0·7, 0·85, and 0·5 respectively, from proximal phalanx to claw inclusive; middle toe, 1·3, 1·0, 1·1, and 0·6; and inside toe, proximal joint, 1·3; next, 1·15; and the claw, 0·55 cm. long.

It remains for me now, so far as the genera *Brachyrhamphus*, *Synthliborhamphus*, and *Cepphus* are concerned, to present, in the form of a brief synopsis, the osteological characters which seem to distinguish them. These may be compared with other synopses given above for *Alca* and *Uria*.

Comparative Synopses of the Osteological Characters of the three Genera Brachyrhamphus, Synthliborhamphus, and Cepphus.

My material permits me to deduce these characters from *B. marmoratus*, *S. antiquus*, and *Cepphus grylle*. Additional

remarks will be found above, also, upon the pectoral arch and sternum of *C. columba.*

Brachyrhamphus marmoratus has all the general characters of a Guillemot, but differs from *Uria* in having its *vomer* produced anteriorly in a spine. Peculiar wing-like post-frontals formed by the superior orbital margins having been absorbed by the supraoccipital glandular depressions. Crotaphyte fossæ *lateral* not meeting the supra-occipital prominence behind. Ramal vacuity patulous (always ?). First pair of free pleurapophyses on the *thirteenth* vertebra. Pelvis broad and short in comparison, with thirteen vertebræ in its sacrum; one pair of sacral ribs, three sesamoids about the elbow. Upper half of tibia and fibula slightly rotated outwards. Possesses an anchylosed accessory metatarsal process.

Synthliborhamphus antiquus.—All the general characters of the Guillemots, with a few distinguishing ones—vomer, crotaphyte fossæ, post-frontals as in the last. Lower two-thirds of tarso-metatarsus laterally compressed as compared with other *Alcidæ* (and, as a negative character, the accessory metatarsal process absent).

Cepphus grylle.—Spine at the anterior end of vomer better marked (like in the *Laridæ*). Crotaphyte fossæ reach the supraoccipital prominence; post-frontals as in the last. Maxillary plates pierced by a circular foramen in each case.

Xiphoidal extremity of sternum more expanded, 1-notched, and over the inner margin of each one or two foramina on either side. Twelve sacral vertebræ in the pelvis (including in the count, as I have in other cases, the dorso-lumbar and uro-sacral).

Pelvis approaches the form of that bone in the Puffins.

Inner fibular ridge of the outer condyle of the femur very prominent.

Note.—The next Part will be devoted to some observations upon the osteology of the Auklets.

ON THE MINUTE ANATOMY OF THE VAGUS NERVE IN SELACHIANS, WITH REMARKS ON THE SEGMENTAL VALUE OF THE CRANIAL NERVES.

By THOMAS W. SHORE, M.D., B.Sc., *Lecturer on Comparative Anatomy and Demonstrator of Physiology at St Bartholomew's Medical School.* (PLATES XX., XXI.)

(From the Biological Department of St Bartholomew's Hospital.)

IN a former paper,[1] published a year ago, I gave a summary of our present knowledge of the anatomy and development of the vagus in Petromyzon, in Elasmobranchs, in Rana, and in the Amniota, and arrived at the conclusion that the generally accepted ideas as to the morphological character of this nerve are open to doubt. Though not altogether proved, I showed from the facts then before me that the following propositions were highly probable:—

1. "That the vagus is a 'compound nerve,' but not in the sense generally supposed; it is, rather, a compound of the visceral rami of the anterior spinal nerves and the remnants of the brain-ganglia and lateral cords of the nervous system of Invertebrata, than of several metameric nerves."

"3. That the visceral part of the vagus of Fishes includes the branchial nerves, and has arisen from a coalescence of the visceral rami of the anterior spinal nerve-segments, the corresponding motor and sensory somatic branches of which remained separate."

3. "That the ganglia of the cranial nerves (5th, 7th, 9th, and 10th) are the representatives of the brain-lobes of Nemertea, and probably of the cerebral ganglia of Annelida and Arthropoda."

4. "That the 'ramus lateralis' is of extreme ancestral origin, and is equivalent to the lateral strands in the nerve plexus of Nemertea, to the main nervous system of Annelida and Arthropoda, and possibly also to the nerve ring of Cœlenterata."

I further pointed out the direction in which investigation should proceed to test these propositions. During the past twelve months my time has been chiefly occupied with other matters, but I have been able to make some observations on these questions. I have chiefly worked with the vagus nerve of the Skate (*Raia batis* and *R. clav.*), and the results which I am about to describe refer particularly to this type, though isolated

[1] "On the Morphology of the Vagus," *Jour. of Anat. and Phys.*, 1888.

observations I have been able to make on other Selachians tend to show that they apply generally.

A. *Preliminary, Historical, and Critical.*

Since the publication of Gegenbaur's memoir[1] on the cranial nerves in Hexanchus, the arrangement, structure, and development of the cerebral nerves have been considered as of the greatest importance in connection with the question of the segmentation of the Vertebrate head, and also to some extent in relation to the question of the ancestry of the Chordata. Most previous workers have come to results which they interpret as showing that the majority of the cranial nerves are "segmental." In fact, excepting perhaps the optic, all the cranial nerves have by some observer or other been considered to be of this nature. Any doubt as to the exact segmental value of these nerves should be strictly and completely analysed. It appeared to me, from the facts established by previous observers, that many of the conclusions which they have arrived at are strained, and hardly justified by the facts brought forward.

Until quite recently the spinal metameric nerves have been regarded as composed of two roots only—dorsal or sensory and ganglionated and ventral or motor and non-ganglionated—which, after joining to form a common trunk, divide into the dorsal and ventral branches. On comparing the cranial nerves with the spinal, the plan of construction at first sight appeared to be very different; but a careful examination of them by Gegenbaur[2] seemed to show that they could be arranged into two sets—(1) comprising the olfactory and optic, and having no resemblance to spinal nerves; and (2) including all the rest of the cranial nerves which agree more or less with the spinal nerves, or could be derived from the plan of a spinal nerve. Proceeding on the supposition that the nerves in this second set were homodynamous with spinal nerves, he explained their peculiarities as being the result of one or more of the following changes:—(*a*) increased development of some of the branches of a cranial metameric nerve, with degeneration of others; (*b*) non-union together of the dorsal and ventral roots of a metameric cranial nerve, so that the two roots appear to be separate nerves; (*c*) concrescence together of nerves representing two or more metamers, so as to appear as one nerve. Following this plan, he thought that the second set of cranial nerves fell into two groups, viz.—(*a*) the *trigeminal group*, including

[1] "Ueber die Kopfnerven von Hexanchus, &c.," *Jenaische Zeitschrift*, Bd. vi. 1871.

[2] *Elements of Comparative Anatomy*, English translation, by Jeffery Bell, 1878.

two nerves—trigeminus, with the oculomotorius and trochlearis both of which he regarded as parts separated off from it; and the facialis-acousticus, with the abducens which he believed to have been segregated from it; (β) the *vagus group*, made up of two nerves—glossopharyngeal and vagus. In the case of the last of these the process of concrescence is believed to have been most marked, for this nerve is regarded as a complex of several metameric nerves homodynamous with spinal nerves.

When, however, it was discovered by Balfour[1] and Milnes Marshall[2] that the spinal dorsal roots are developed as outgrowths from a neural ridge or crest, and the ventral roots as outgrowths from the cord, and that certain of the cranial nerves arise from a neural crest whilst others do not, a definite basis of comparison arose. Those cranial nerves which were shown to arise from a neural crest were regarded as the cranial equivalents of the dorsal spinal roots, and therefore, as indicating so many corresponding head segments, and the rest of the cranial nerves were considered to be the equivalents of the ventral spinal roots, or to be some distinct formation not entering into the comparison at all. By Marshall, the differences between the cranial and spinal nerves were explained by the supposition that the cranial nerve-metamers, originally constructed on the plan of the spinal, had become split up into their elements and rearranged, so that it had become difficult to trace the corresponding dorsal and ventral roots. But Balfour did not agree with this, for some of the supposed dorsal cranial roots are motor, some sensory, and some mixed. Thus one of the fundamental tests in the comparison failed. Balfour,[3] finding that the dorsal and ventral roots of the spinal nerves in Elasmobranchs arise alternately, and not in the same vertical plane, and that the same is the case in Amphioxus, and observing, as he thought,[4] that in Amphioxus only one set of roots (those arising from the dorsal side) are present on each side, formulated the hypothesis, that the cranial nerves were evolved, not from a plan identical with that of the *existing* spinal region, but from a series of *mixed* metameric nerves, with one root of origin only, which existed in spinal and cranial regions alike, and from which both arrangements were independently evolved. On this theory, those cranial nerves which are developed from a neural crest were identified as equivalent either to a *whole*, or to the dorsal part of a spinal nerve, and were believed to indicate head segments as much as the spinal nerves indicate body segments.

[1] *A Monograph on the Development of Elasmobranch Fishes*, London, 1878; also "On the Development of the Spinal Nerves in Elasmobranch Fishes," *Phil. Trans.*, 1876.

[2] "On the Early Stages of Development of the Nerves in Birds," *Jour. Anat. and Phys.* 1877; also "On the Development of the Cranial Nerves in Chick," *Quart. Jour. Micr. Sci.*, 1878.

[3] *A Monograph on the Development of Elasmobranch Fishes.*

[4] It has subsequently been shown that the Amphioxus possesses separate alternating dorsal and ventral nerve roots. *Vide* Rohon, "Untersuch. über *Amphioxus lanceolatus*," *Denksch. d. k. Akad. d. wiss. Wien.*, B. xlv.

In the endeavours of various workers to determine the *number* of head segments, the arrangement, mode of origin, and distribution of these cranial nerves have held a most prominent place. By Milnes Marshall,[1] a segmental cranial nerve was held to have the following characters:—

(1) It is developed from the neural crest.
(2) Later on, it shifts downwards to the side of the brain.
(3) In the early stages it has a ganglionic swelling on its root or near its origin.
(4) Its course is more or less at right angles to the long axis of the head.
(5) It supplies the two sides of a gill-cleft, or its equivalent.

These characters have been demonstrated in the case of the fifth, the facial, the glossopharyngeal, and other nerves, all of which are, therefore, regarded as "segmental." In applying these tests to the olfactory nerve, Marshall's argument is not at all conclusive, for he does not *prove* that the nerve arises from the neural crest, and he regards the olfactory organ as a gill-slit on the insufficient grounds that it appears at about the same as the post-oral gill-slits, and that the folds of the Schneiderian membrane much resemble the gill-folds on a branchial arch.

Marshall[2] subsequently introduced a new element in the determination of the number of head segments, and in deciding the question as to how far the cranial nerves which are believed to be "segmental" are really so. He found that certain of the cranial nerves in Elasmobranchs had definite relations to the cranial parts of the cœlom, or "head-cavities." These head-cavities had been previously described by Balfour,[3] who found a premandibular, a mandibular, a hyoidean, and several branchial cavities. According to Balfour, there is at first a simple undivided prolongation of the cœlom into the head region, extending as far forwards as the optic vesicles. It then becomes divided into two parts by a constriction produced by the developing spiracular slits. The anterior part then divides into two by a constriction along the line of the developing mouth, the posterior part being divided by successively formed gill-slits, so that there is eventually found a series of cavities,—one in each visceral arch and one in front of the mouth. Marshall confirmed Balfour on these points, and also showed that the head-cavities are at an early stage dorsally in communication with each other above the level of the gill-slits, though separate ventrally. He also found that, later on, they become distinct dorsally by separation along dorsal continuations of the lines of the visceral slits, and that, later still, the dorsal parts become separate

[1] "Morphology of the Vertebrate Olfactory Organ, *Quart. Jour. Micr. Sci.*, 1879.

[2] "On the Head-Cavities and Associated Nerves in Elasmobranchs," *Quart. Jour. Micr. Sci.*, 1881.

[3] *Loc. cit.*, p. 206.

from the ventral; but this he observed in the first three only. Marshall also showed that the 3rd, 5th, and 7th nerves lie just behind the 1st, 2nd, and 3rd head-cavities respectively; but it was difficult to be quite sure of the relations of nerves to the hinder head-cavities. It is thus clear, if the head-cavities indicate true somites, that the nerves mentioned are "segmental." But do these head-cavities represent true somites of the head, of equal value with those of the trunk? Marshall thought that the dorsal parts which he observed to become separated from the ventral in the cases of the first three head cavities might represent protovertebræ of the trunk region, and he expressed his opinion, though he had not quite proved the point, that the eye muscles are developed from these dorsal parts of the first three head cavities.

Van Wijhe[1] has considerably extended the observations of Balfour and Milnes Marshall on the mesoblast of the Selachian head. He has described segments in the head which he considers to be homologous with the vertebral somites of the trunk. He finds *nine* such head somites. In addition to these nine head somites, the mesoblast of the head region, in its lateral and ventral parts, is said to be formed into a series of lateral plates, comparable to the latero-ventral unsegmented sheets of mesoblast of the trunk region. These lateral plates of the head agree with the corresponding parts of the trunk, in enclosing a cœlom or "head cavity," but differ in that the head cavity is split up into as many cavities as there are visceral arches. Each dorsal head myomere of Van Wijhe is, at an early stage, hollow, its cavity communicating with the space in a visceral arch, as is the case at an early stage in the trunk where the cœlom sends dorsal prolongations into the vertebral somites. The first somite of the head, also, has a ventral prolongation, though there is no visceral arch, and its cavity appears to be the same as Balfour and Marshall called the premandibular head cavity. According to Van Wijhe's description and drawings, there appears to be only one visceral arch cavity corresponding to what he regards as the 3rd and 4th myomeres. Thus, whilst he finds nine myomeres, there are only six lateral visceral-arch cavities, for the hindermost is not differentiated from the pericardial portion of the general cœlom, and the ventral part of the first myomere does not lie in a visceral arch. Balfour and Marshall, then, described a segmentation of the mesoblast of the head, which was such that it *followed exactly the visceral arch segmentation, and was developmentally shown to be due to the formation of the visceral slits*, whilst Van Wijhe found one which he believed to be quite *independent of the visceral slits.* From the two sets of mesoderm segments of the head, Van Wijhe found that, two sets of muscles, innervated by different sets of nerve roots, are formed. The dorsal nerve roots are sensory, and also *innervate muscles derived from the lateral plates, i.e.*, from the walls of the various visceral-arch cavities, whilst the ventral nerve roots are motor, and supply entirely *the muscles derived from the dorsal myomeres.*

[1] "Ueber die Mesodermsegmente und die Entwickelung der Nerven des Selachierkopfes," *König. Akad. der Wiss. zu Amsterdam*, 1882.

From Balfour's discovery of head cavities, extended by the observations of Marshall and Van Wijhe, there arose a more definite basis of comparison of cranial with spinal nerves; for it is obvious that, so long as the arrangement of nerves with respect to gill-slits, formed the basis on which they were declared to be segmental in the head region, and the relation of nerves to myomeres was the basis of segmental significance in the spinal region, no common ground of comparison existed.

Van Wijhe's results are thus tabulated :—

Myomere.	Muscles developed from Myomere.	Ventral Nerve Root.	Dorsal Nerve Root.
1.	Rect. sup. int. inf. and obl. inf.	Oculomotor.	Ophthal. profund.
2.	Obl. superior.	Trochlear.	Trigeminus *minus* ophth. prof.
3.	Rect. extern.	Abducens.	Acoust. facialis.
4.	None.	None.	
5.	None.	None.	Glossopharyng.
6.	Very rudimentary.	None.	Vagus.
7.	Muscles extending from skull to shoulder-girdle.	Hypoglossal.	Vagus.
8.			
9.			

But some doubt has already been thrown on Van Wijhe's results by Dohrn,[1] who differs from him as well as from Marshall in not regarding the dorsal parts of the head cavities as equivalent to protovertebræ. He considers *both* the dorsal and ventral parts of the head cavities to be homologous with the walls of the body cavity in the trunk region. The muscles of the eyeballs he therefore holds to be homologues of branchial muscles. He finds in the lens of the eye a pre-oral gill-slit, through which light originally came to the eye. He throws great doubt on the possibility of estimating the number of somites of the head; for he believes that all the parts of the head except the brain are ventral structures, just as the tail contains nothing but dorsal structures. The cranial nerves have, he thinks, lost those branches which supply the dorsal somites, and those to the ventral structures have undergone complication from alteration of the positions of the gill arches.

It seems to me, from Van Wijhe's drawings, that he has not clearly proved that what he believes to be myomeres are really morphologically distinct from the ventral "visceral-bogenhöhle." It is of course a strong argument in favour of the separate existence of myomeres if they are found not to correspond to the visceral arch cavities; and Van Wijhe's drawings show only one "visceral-bogenhöhle" to what he calls the 3rd and 4th myomeres. A reference to figs. 1 and 2 of his paper will show that these two myomeres are the least clearly

[1] "Zur Phylogenese des Wirbelthierauges," *Mittheil. a. d. Zool. Stat. zu Neapel*, 1885.

marked of all, and it is quite possible that what he has interpreted as two dorsal segments are really only one. In no other of his figures does he show somites 3 and 4 as separate structures, though it is obvious from figs. 8 and 11 that his somite 3 corresponds to his second visceral arch cavity. I very much doubt the existence of the 4th of Van Wijhe's dorsal segments. It is also clear, from the figures in his paper, that the first three "somites," which are obviously the same as the anterior three of Balfour's and Marshall's head cavities, are lined by an epithelium of a single layer of cells identical with that lining the pericardial cavity, whilst they present a very different appearance to what Van Wijhe calls somites 6, 7, 8, and 9. The last four of his head myomeres are very like those of the trunk region, As to somite 5, it is in Van Wijhe's figures never very marked, and seems to early disappear, though the corresponding visceral arch cavity is fairly distinct. It is not clear that somite 5 is ever distinct from the 3rd "visceral-bogenhöhle." A reference to the table on p. 383 shows that no ventral nerve root and no muscle formation was observed by Van Wijhe in connection with somites 4 and 5, which fact seems to me to throw doubt on the accuracy of his conclusions as to their existence. It seems to me, then, that Van Wijhe has not established the existence of what he calls somites 1–5; whilst it would appear that the cavities of somites 1, 2, and 3 are merely the dorsal parts of the sections of the head cavity in this region, and *not equivalent to true myomeres.* As to Van Wijhe's somites 6, 7, 8, and 9, which in his figures clearly resemble protovertebræ, I would point out that Balfour had observed muscle-plates in this region, which he was inclined to believe were really spinal segments that had to some extent overlapped the posterior part of the head.[1]

If, as I think, Van Wijhe's somites are not clearly established, we have in them no sure basis on which to compare together cranial and spinal nerves.

Beard[2] brought into prominence another consideration by which the cranial nerves could be compared with each other, based on what he now calls the "branchial sense organs," commonly known as the "sense organs of the lateral line." At one time Beard himself spoke of these as "segmental sense organs," but now he prefers the above name, for, although segmental in their arrangement, he endeavours to show that they are primarily confined to the gill-slit region of the body. In a former paper[3] on this subject, Beard believed these sense organs to have had a connection with the posterior roots of spinal nerves; the object of this hypothesis being to explain the backward extension of the lateralis vagi nerve. He discards this in the paper now under review. If, then, the sense organs of the lateral line are primarily confined to the cranial and gill-slit regions, they can afford no basis on which cranial can be compared with spinal

[1] *Loc. cit.*, p. 209.

[2] "The System of the Branchial Sense Organs, &c., in Ichthyopsida," *Quart. Jour. Micr. Sci.*, 1885.

[3] "On the Segmental Sense Organs, &c.," *Zool. Anz.*, Nos. 161 and 162, 1884.

nerves. Beard himself points this out, for he regards the spinal and cranial segmental nerves as from the first essentially different, and as being separately evolved from an original simple plan. Beard considers that a typical cranial segmental nerve has the following characters:—(1) It arises from the neural crest; (2) then grows downwards to the dorsal side of a gill-cleft; (3) it fuses with the external epiblast just above a gill-cleft; (4) a thickening of epiblast forms at this spot, and subsequently gives rise to (*a*) the ganglion of the nerve, (*b*) the dorsal or "supra-branchial" branch, and (*c*) the corresponding sense organ; (5) the main stem which has arisen from the neural crest continues as the ventral branch, and passes to the posterior side of the corresponding gill-cleft forming the post-branchial branch; (6) the prebranchial, and possibly the pharyngeal branches, subsequently form by separation from the skin. He endeavours to bring all the cranial nerves, except the optic, under this scheme, the common plan being the presence of a sense organ over each gill-slit, and the development of the nerve in two parts, viz., (*a*) from the neural crest, and (*b*) directly from the same epiblastic thickening as gives rise to the sense organ. In applying this test, however, he falls into the logical error, which was pointed out by Miss Johnson and Miss Sheldon,[1] of taking the gill-slits in one part of the head to prove that the sense organs and their nerves are segmental and branchial, and the sense organs in another part of the head as evidence of one or more aborted gill-clefts. He draws conclusions which I do not think his facts warrant. For example, the fact that the sensory skin thickening in relation to the 7th nerve, though at first single, becomes divided, as it grows forwards, into two, with a simultaneous division of the dorsal nerve into two (*ram. ophth. superfic* and *ram. buccalis*), is taken as evidence of the existence of two segments corresponding to the facial nerve, and as sufficient grounds to postulate the former existence of a now aborted gill-slit. Again, the olfactory nerve is considered to be segmental, and the olfactory organ a "branchial sense organ," on the very insufficient grounds that the nerve grows from the brain (though it is not shown to arise from the neural crest) and joins a thickening of external epiblast from which there arises the olfactory organ and a ganglion for the nerve. The absence of a dorsal and a ventral branch, as well as of a gill-slit, and in a region in front of the mouth where there is *à priori* reason for believing that gill-slits never existed, is not considered sufficient to negative such a view. The auditory nerve, also, is said to represent a segment apart from the facial, and the auditory organ a branchial sense organ, for reasons precisely similar to the case of the olfactory, and the entire absence of both dorsal and ventral branches and of a gill-slit, as well as the common origin of the nerve with the facial, are not considered conclusive evidence against such a view. Beard thus takes up what appears to me to be an untenable position, that the *single* facio-auditory outgrowth from the neural crest really corresponds to *three* head segments, notwithstanding that there is *only one gill-slit!*

[1] "Development of the Newt," *Quart. Jour. Micr. Sci.*, 1886.

In my opinion, Beard's "branchial sense organs" form a very uncertain guide to the number of head segments, whilst it is clear also that they afford no basis on which cranial can be compared with spinal nerves.

The above summary represents the state of our knowledge on the comparative value of the cranial and spinal nerves, so long as we regard a typical spinal nerve as being composed of two roots only. But it is now clear, from the researches of Gaskell,[1] that a complete spinal nerve-metamer is composed of a third root also, the fibres of which, however, are not distinct from the dorsal and ventral roots except in the upper cervical region, where the spinal roots of the spinal accessory nerve of Mammals represent it. This third root is the *lateral* one, and contains the fibres which innervate the *visceral* system of muscles, including those derived from the lateral plates of mesoblast, and the endodermal surface. The ventral root innervates the *somatic* system of muscles, *i.e.*, those derived from the dorsal vertebral somites; and the dorsal root supplies the ectodermal surface. A complete spinal nerve-metamer is thus shown to be composed of—

1. A somatic motor root.
2. A somatic sensory root.
3. A splanchnic motor root.
4. A splanchnic sensory root.

Gaskell further shows that the somatic motor root is non-ganglionated, whilst the splanchnic motor root is divisible into two parts—the ganglionated and non-ganglionated. Both the somatic sensory and splanchnic sensory roots are ganglionated. The ganglia of the somatic and splanchnic sensory roots are what have hitherto been known as the ganglia of the dorsal nerve roots, whilst the ganglia of the ganglionated part of the splanchnic motor root are the ganglia of what is generally called the sympathetic system. The two sets of ganglia have different characters—those of the sensory somatic and splanchnic roots are *stationary*, whilst those of the splanchnic motor roots are *vagrant*. Gaskell also showed that the fibres of the ganglionated splanchnic root can be traced in a mixed nerve bundle by the fact that though they are medullated, like the ordinary somatic motor and sensory fibres, yet they are very much smaller. The ordinary somatic fibres in the Dog have a size varying from 14·4 μ to 19 μ, whilst the splanchnic motor fibres (ganglionated portion) vary in size from 1·8 μ to 3·6 μ.[2] The ganglionated splanchnic motor fibres are further distinct from the non-ganglionated by the fact that they join the ganglion cells of the so-called sympathetic ganglia, and there lose their medullary sheaths, emerging as non-medullated fibres. The non-ganglionated motor splanchnic fibres do not join the sympathetic ganglia, but pass off to innervate the muscles derived from the lateral plates of mesoblast.

[1] "On the Structure, Distribution, and Function of the Nerves which Innervate the Visceral and Vascular Systems," *Jour. of Phys.*, vol. vii. 1886.

[2] $\mu = \frac{1}{1000}$th of a millimetre.

Here we have a new and definite basis on which we can compare cranial and spinal nerves. Before a cranial nerve can be regarded as representing a complete metamer of the same value as a spinal one, it must be shown to contain all the above four sets of fibres, and we must be able to trace a splanchnic ganglion as well as a somatic one. Gaskell[1] himself has endeavoured to apply these principles to the cranial nerves in Man, Dog, and Sheep; and, leaving out of consideration the olfactory, optic, and auditory nerves, has arrived at the following results:—

1. The *third nerve* contains large and small medullated fibres, the former passing to the eye muscles supplied by this nerve, the latter going to the ciliary ganglion, which is thus identified as the vagrant root ganglion of the splanchnic fibres of a nerve-segment. Near to the brain, on the rootlets of the nerve, there are found evidences of a *degenerate ganglion*, which Gaskell identifies as the ganglion of the now functionless posterior root corresponding to the third nerve. This nerve thus conforms to the type of a complete metameric nerve.

2. The *fourth nerve* has also two sets of fibres (small as well as large medullated), and possesses evidence of a degenerate posterior root ganglion. The small fibred portion of the nerve has not, however, yet been traced to any vagrant splanchnic ganglion.

3. The *sixth nerve* probably has the same structure, though the small fibres are much more doubtful than in the case of the 3rd and 4th nerves, and the degenerate posterior root ganglion is also doubtful.

4. The *motor root of the fifth nerve* contains small and large medullated fibres. The former are believed to go to the spheno-palatine ganglion, though they have not yet been traced there. If this is the case, this ganglion will represent the vagrant splanchnic ganglion of a nerve metamer. A degenerate posterior root ganglion, like that of the preceding nerves, has been found. The motor root of the 5th is, therefore, not of the nature of a ventral root, but contains evidence of being in itself a *complete metameric nerve.*

5. The *seventh nerve* contains a small as well as a large medullated portion, the former passing to the ganglion cells of the ganglion geniculatum, and a degenerate posterior root ganglion is found close after the exit of the nerve roots from the brain.

The above *five* nerves conform to one type, having a *degenerate posterior root ganglion* and a well-marked *vagrant* ganglion.

6. The nerves arising from the medulla have not the same arrangement as the above, for there is here, not *degeneration* of any component parts, but *separation* of the elements of one or more spinal nerves, so that the separate nerves do not each represent a complete metamer.

7. The separation is believed to bear an intimate connection with the making good of the loss of the sensory elements of the preceding nerves.

8. The *sensory root of the fifth nerve* possesses a well-marked and

[1] "On the Relation between the Structure, Function, and Distribution of the Cranial Nerves," *Proc. Roy. Soc.*, 1888.

functional somatic posterior root ganglion, the Gasserian, whilst it has no splanchnic small medullated fibres and no vagrant ganglion.

9. The *ninth nerve* has a *splanchnic* sensory root ganglion,—the ganglion jugulare,—but no somatic sensory one; whilst the ganglion petrosum is the ganglion of the small medullated splanchnic motor fibres of this nerve. There are no somatic motor or sensory fibres.

10. The *tenth nerve*, similarly, has no somatic sensory root fibres or ganglion, except those forming the auricular nerve. The ganglion jugulare is the splanchnic sensory ganglion. The ganglion trunci vagi is the ganglion of the splanchnic motor small medulated fibres.

11. The *eleventh nerve* contains small medullated splanchnic motor fibres, which join the ganglion trunci vagi, and large medullated splanchnic *non-ganglionated* ones, which supply the pharyngeal, laryngeal, and spinal accessory group of muscles. There are no somatic sensory or motor fibres.

12. Neither in the ninth, nor tenth, nor eleventh are there any somatic fibres. The motor non-ganglionated somatic roots are found exclusively in the *twelfth nerve*.

These conclusions lead one to infer that the 3rd, 4th, motor part of 5th, 6th, and 7th nerves are complete metameric nerves, *each* of equal value with one spinal nerve-metamer, whilst the group containing the 5th (sensory), 9th, 10th, 11th, and 12th nerves are *together* composed of the parts of one or more perfect spinal nerve metamers, whose elements have been scattered.

A similar examination of the cranial nerves in more primitive types, like Selachians, which is more likely to throw light on the segmentation of the Vertebrate head than an examination of Mammals, has not, to my knowledge, yet been made.

I have commenced the examination of the cranial nerves of the Skate and other Selachians from this point of view, but at present have had time only to deal with the vagus. The following account is a preliminary communication of the results I have been able to arrive at up to the present time.

B. *Minute Anatomy of the Vagus of the Skate.*

Method of Research.—The animals were obtained fresh, and a careful dissection of the whole nerve made from the dorsal aspect. When exposed, it was removed entire with a portion of the medulla, so as to preserve the normal position of the nerve roots, and spread out in natural position as far as possible, on a sheet of glass. Some 1 per cent. solution of osmic acid was poured over it, and a careful drawing was then made. The

nerve was then cut up into suitable pieces, which were placed in 1 per cent. solution of osmic acid in separate bottles. Osmic acid was allowed to act on the nerves for a time, varying with their thickness, generally twelve hours or longer in darkness, the osmic acid being changed once or twice in the case of thicker pieces. My earlier preparations were not sufficiently stained by the osmic acid, and in subsequent ones this was obviated to a great extent by dissecting off as much connective tissue as possible before placing in osmic acid. After staining, the nerves were treated with successive grades of spirit up to absolute. They were then placed in turpentine for a short time, then saturated with solid paraffin and imbedded. Sections were cut in ribbons by the rocking microtome.

A typical Spinal Nerve.—It was first of all necessary to obtain a general idea of the structure of a typical spinal nerve and its roots in the Skate. One or two of the spinal nerves were therefore examined, but only with the object in view of obtaining a standard for purposes of comparison. The typical spinal nerve has two anatomical roots, which perforate the cartilaginous walls of the spinal canal by separate apertures, thus rendering it somewhat difficult to obtain the whole length of both dorsal and ventral roots of a given nerve. The fibres composing these roots are of two kinds, the large medullated ones varying in size from about 17 μ to 25 μ, and the small medullated ones ranging in size from about 2 μ to 8 μ. I have not had time to trace these fibres, but have no doubt that the small medullated fibres pass in the rami communicantes to the so-called sympathetic, which forms a longitudinal cord in close relation with the posterior cardinal vein. It is said that the sympathetic cannot be traced further forwards than the ductus Cuvieri, so that there is no "sympathetic" system near the anterior cardinal vein. This, if it be a fact, taken in conjunction with the fact that the vagus has a relation to the anterior cardinal vein similar to that of the "sympathetic" to the posterior cardinal, supports the idea expressed in my former paper, that the vagus is in the anterior region of the body morphologically equivalent to the sympathetic in the posterior. This idea would be still further supported if, as I suggested in my former paper, it could be shown that the anterior spinal nerves do not contain small

medullated or splanchnic motor fibres. Upon this point I have, however, not had time to satisfy myself, though an isolated observation of one of the nerve roots forming the brachial plexus showed only a very few small medullated fibres.

General External Anatomy of the Vagus.—A drawing, which may be considered typical, of the right vagus of the Skate is given in fig. 1. The nerve arises by a large number of roots from the medulla; these roots are formed into two sets, an anterior[1] group, consisting of from six to ten distinct fasciculi, and a posterior group separated by a definite interval from the anterior set, and forming a broad band not well divided into fasciculi, and arising from the medulla slightly to the ventral side of the rest of the roots. This posterior group of nerve roots must not be confounded with the so-called ventral vagus roots described by Gegenbaur.[2] The ventral roots of Gegenbaur are about three small slender filaments coming from the ventral side of the medulla, and leaving the skull by separate apertures, *quite distinct from the vagus roots.* I have not as yet been able to make a satisfactory examination of the minute anatomy of these ventral roots of Gegenbaur. The two sets of vagus roots join together as the nerve is leaving the skull cavity, and whilst within the cartilage of the skull, but the distinction into the two sets can be traced as a groove along the nerve for some distance. There is *no obvious ganglionic enlargement* upon the vagus roots whilst within the cartilage of the skull, nor on any part of the main trunk of the nerve, though, as will be presently described, nerve cells are present in groups in certain parts of the main trunk. Whilst in the cartilage of the brain-case a slender branch begins to separate from the rest of the nerve roots, and as the nerve emerges from the cartilage of the skull, this branch passes off as the small dorsal ramus, or sometimes it perforates the cartilage by a separate canal of its own. Immediately on leaving the skull the first vagus-branchial nerve[3]

[1] The terms "anterior" and "posterior" are not used in the sense "dorsal" and "ventral," but refer to the position in the animal's body, anterior being in front, posterior behind.

[2] *Elements of Comparative Anatomy*, English translation, p. 520.

[3] I use the terms "vagus-branchial," so as to distinguish the branchial branches of the vagus from the branchial branch of the glosso-pharyngeal. The *first* "vagus-branchial" supplies the *second* gill-cleft.

is given off from the outer side of the main trunk. Upon this

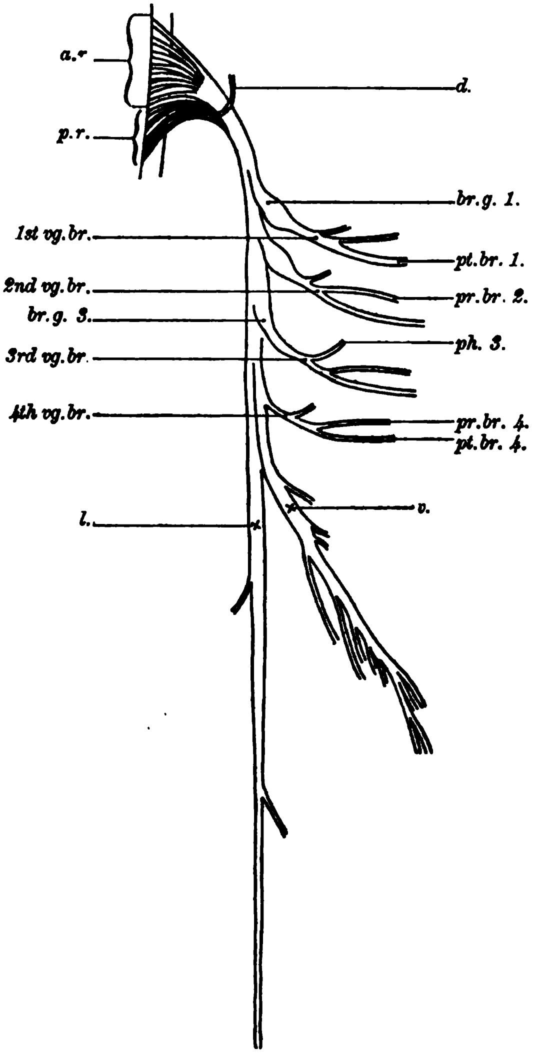


FIG. 1.—Diagram of the right vagus of Raia. *a.r.*, anterior set of root fasciculi; *p.r.*, posterior set of root fasciculi; *d.*, dorsalis branch; *1st, 2nd, 3rd, 4th, vg.br.*, first, &c., vagus-branchials; *br.g. 1, 2, 3*, first, &c., branchial ganglia; *pr.br. 2*, second pre-branchial nerve; *pr.br. 4*, fourth pre-branchial nerve; *pt.br. 1, 4*, first, &c., post-branchial nerve; *ph. 3*, third pharyngeal branch; *l.*, lateralis; *v.*, visceralis.

branch is found a well-marked ganglionic swelling. This

ganglion I propose to call the first "branchial ganglion," those on the other vagus-branchials being respectively the second and third branchial ganglia. In one or two cases the portion of this branch lying on the *proximal side* of the ganglion is very slender—in fact, not half the size of the distal part of the branch. In other cases the ganglion lies quite close to the origin of the branch from the main trunk. From the first vagus-branchial beyond the ganglion a slender *pharyngeal* branch is given off, and shortly afterwards a *prebranchial* trunk running anteriorly to the second gill cavity, the main part of the branch continuing along the posterior wall of the second branchial cavity as the *post-branchial* nerve. Close behind the first vagus-branchial the second one arises, and it has a ganglion, and gives off branches to the sides of the third gill-cavity in the same manner as the first. The third and fourth vagus-branchials are given off lower down and behave like the first and second; but the ganglion of the third is almost indistinguishable from the main trunk, whilst the fourth, which is very slender, has no ganglionic enlargement. As a rule, all the branchial branches leave the main trunk before it divides into its two main subdivisions—*visceralis* and *lateralis*—though the arrangement of the fibres preparatory to this division is seen as a groove on the main trunk for a variable distance; the fourth, and sometimes the third vagus-branchials obviously arising from the portion of the main trunk which continues as the visceralis. I am unable to find the slightest indication that the visceralis fibres are traceable up as a separate fasciculus to that from which the branchial nerves arise, as was stated by Hubrecht[1] to be the case in Elasmobranchs. The visceralis nerve curves ventralwards, and gives off numerous branches, that to the heart being usually easily traceable. The lateralis passes downwards dorsally to the spinal nerves, situated deeply amongst the muscles beneath the lateral line. It can be traced, gradually tapering, and giving off branches to the lateral line to quite the tail region.

The Vagus Roots.—The fibres composing the vagus roots are of three kinds, which can easily be recognised and traced in transverse sections by their sizes. The largest fibres vary in

[1] "The Relation of the Nemertea to the Vertebrata," *Quart. Jour. Micr. Sci.*, p. 638, footnote, 1887.

size from 20 μ to 33 μ, averaging about 25 μ; the medium-sized fibres vary from 12 μ to 18 μ, averaging about 15 μ; and the smallest vary from 2 μ to 10 μ, averaging about 6 μ. They are all medullated; but in the case of the large and the medium-sized fibres the medullary sheaths are thick and well marked, whilst those of the smallest fibres are not nearly so thick or definite. The most anterior fasciculi of the anterior set of roots are composed almost exclusively of the medium-sized fibres, the rest of the fasciculi of the anterior set of roots being made up largely of the smallest fibres, with a sparing admixture of the medium-sized fibres. The posterior set of roots is composed almost exclusively of the largest kind of fibres, with a small proportion of medium-sized fibres. With a $\frac{1}{2}$ or $\frac{2}{3}$ inch objective the appearances presented by transverse sections of the root fasciculi, in which the three kinds of fibres respectively predominate, are markedly different. These appearances, and the arrangements of the root fasciculi, are shown in Pl. XX. fig. 2. The fibres, as seen in transverse sections with a $\frac{1}{8}$-inch objective, are shown in figs. 3, 4, and 5. On tracing, by a series of sections, the fibres composing the various root fasciculi, they are found to arrange themselves into two main strands—one composed of all the large fibres of the posterior set of roots, with several of the small fibred fasciculi of the anterior set; the other made up of the fibres of the anterior set of roots, and composed of medium and small fibres. These two strands become united within the cartilaginous canal in the skull, and the fibres mingled together; the large fibres, however, in the main keep together, though not in a separate sheath, and come to lie at the inner side of the main trunk; the other fibres are more scattered, but the medium-sized ones keep chiefly to the outer side of the main trunk. A small fasciculus of fibres, of the average size of from 20 μ to 25 μ, which obviously forms the hindermost bundle of the posterior set of roots, does not become so intimately united with the rest of the nerve as do the other posterior fasciculi. These fibres eventually pass into the small dorsal branch of the vagus, which is well known to be sensory to a small part of the body surface in the occipital region. In the course of this small fasciculus *there are found a few ganglion cells*, but what relation they have to the fibres I have not been

able to discover. I have little doubt that these fibres are the homologues of the somatic sensory fibres, and the ganglion cells the *equivalent of a posterior root ganglion* (stationary) of a typical spinal nerve. If this be so, then the homology of the small dorsal branch with the auricular nerve of human anatomy, and the homology of the small group of ganglion cells with the ganglion jugulare of the vagus of Mammals, is highly probable. Gaskell, however, regards the ganglion jugulare of the vagus of Mammals as equivalent to the ganglion of the *splanchnic* sensory roots. *There are no other ganglion cells, nor any traces of degenerate ganglia in any other of the root fasciculi, or of the proximal part of the main trunk formed by their union.*

The Main Trunk before its division into "Visceralis" and "Lateralis."—The grouping of the fibres of the nerve roots, just described, becomes more and more definite as we pass down the main trunk. At first the parts which are to form visceralis and lateralis respectively are not marked off from each other by any definite band of connective tissue, though quite distinct by the sizes of the fibres; but gradually a very obvious separation into these two parts appears some considerable distance before the two main branches separate from each other. The "lateralis" fasciculus is composed almost entirely of the largest fibres, whilst the other part of the nerve contains almost exclusively the medium and small ones. As we pass downwards the gradual grouping of the fibres, preparatory to the giving off of each successive branchial nerve, is very obvious. In the case of all the vagus-branchial nerves, it is clear that the fibres composing it *are derived exclusively from the same group as will eventually pass on into the "visceralis" nerve.* In the case of the first three vagus-branchials, soon after the group of fibres which will form the corresponding branchial has become distinct, a large number of nerve cells make their appearance, and are exclusively confined to that portion of the visceral fibres which are about to separate as the corresponding branchial. These ganglion cells are, in the case of the first two vagus-branchials, continued for some distance along the branch, and form the corresponding "branchial ganglion." Sometimes there are no nerve cells in relation to the fibres of the first vagus-branchial

until long after the branch has separated from the main nerve. Usually, in the case of the third vagus-branchial, the ganglion cells cannot be traced far along the nerve after it has separated; and in the case of the fourth vagus-branchial, not only is the grouping of fibres, preparatory to its separation, not nearly so obvious as in the cases of the anterior three, but the ganglion cells in relation to it are *confluent with those of the visceralis part of the main trunk*, for it is just below the origin of the third vagus-branchial that nerve cells (apart from those of the branchial groups of fibres) first make their appearance in the main trunk. There thus appears to be some variation, not only in different specimens, but also in the various branchials of the same nerve, in the exact arrangement of the ganglion cells with respect to the main visceralis fasciculus and its branchial branches. Speaking generally, the lower we pass down the main nerve the less differentiated off from those of the main trunk do the ganglia of the branchial nerves become.

Just about the origin of the third vagus-branchial, ganglion cells of the visceralis begin to appear, and are continued without interruption, after the last branchial leaves the main trunk along the visceralis fasciculus, both before and after its separation from the lateralis. At about the same level there appears in the main trunk another group of nerve cells, which, however, is not so distinct or so extensive as the visceralis group. These lie at quite the opposite side of the nerve, amongst the large fibres of the "lateralis" fasciculus, and are continued for a short distance along the "lateralis" when it has separated as a distinct nerve. These two groups of nerve cells I will respectively speak of as the "visceralis-ganglion" and the "lateralis-ganglion."

The Vagus-Branchial Nerves.—It has already been said that these arise exclusively from the fasciculus of fibres which continues afterwards as the "visceralis." They are thus seen to be composed of medium and small sized fibres. The medium-sized fibres, in the main, pass onwards without joining the cells of the branchial ganglia. The small fibres, on the other hand, largely become connected with the cells of these ganglia, from which they emerge *increased in number*, still as small *medullated* fibres. The nerve beyond the branchial ganglion is composed of a very large fasciculus of these small fibres, and,

in a separate sheath, a fasciculus of medium-sized ones. The first branch to be given off is the pharyngeal, which is made up entirely of small medullated fibres, except in the case of the third branchial, which appears to give off some medium-sized ones also in its pharyngeal branch. Almost immediately after the pharyngeal ramus has left the branchial nerve, there appears amongst the remaining small fibres a well-marked group of ganglion cells, *quite distinct from the branchial ganglion* already described. These are continued along the prebranchial branch, which is shortly given off from the main branchial, for a variable distance. The fibres appear to become connected with these cells, which I will speak of as the "prebranchial ganglion." There is such a ganglion present in the case of all the vagus-branchials, but it is most obvious in the cases of the first three. The post-branchial branch is composed of two fasciculi, one of small and the other of medium-sized fibres, the latter being the most posterior in position. The fourth vagus-branchial, however, is different to the others in *not containing any medium-sized fibres*, and in being in all respects much smaller and ill-developed.

In my former paper on the vagus, I expressed the opinion that the branchial branches of this nerve must be considered to be part of its visceral distribution, and that probably the branchial nerves were formed by the separation of the splanchnic rami of some of the anterior spinal nerves, from their corresponding somatic rami, in relation to the Chordate respiratory system. If this is so, we should find that the branchial branches contain not only the same kinds of fibres as the "visceralis," but also the typical elements of the splanchnic system of nerves. These opinions appear to me to be completely proved by the description I have given above of the arrangement of the fibres of these nerves and the position of the various groups of ganglion cells. Each vagus-branchial contains fine medullated splanchnic fibres, which join ganglion cells of either a proximal or a distal set of ganglia—in fact, possesses the typical plan of the so-called sympathetic system. The branchial ganglia are comparable to, and are probably morphologically equivalent to, what Gaskell[1] has called the vertebral or lateral set of ganglia

[1] *Jour. of Phys.*, 1886.

of the sympathetic, and the prebranchial ganglia are the equivalents in every sense to the prevertebral or collateral set of ganglia of the so-called sympathetic system. The fibres which join the cells of these ganglia in the case of the sympathetic of Mammals emerge as *non-medullated* fibres, whilst in the case of the vagus-branchial ganglia of the Skate they emerge as *small medullated* ones. This, however, is not so important a difference as may at first sight appear, for a similar fact has been observed by Gaskell[1] in the case of the splanchnic fibres of the 3rd cranial nerve, where the small medullated fibres which join the cells of the ciliary ganglion emerge, *not as non-medullated, but as fine medullated fibres.* The vagus-branchials of the Skate, however, differ from the typical splanchnic ganglionated system of Mammals in the important particular that they contain some medium-sized fibres of the average dimensions of 15 μ, which are not present in the "sympathetic" of Mammals. These fibres, which do not appear to me to have any ganglia in connection with them, are in my opinion equivalent to the non-ganglionated large-fibred splanchnic portion of the lateral root of Gaskell. Now, we know that in Mammals the spinal accessory nerve is composed of both ganglionated and non-ganglionated splanchnic fibres, and that the latter pass to certain of the muscles of respiration. I therefore suggest, though I do not lay much stress on the point, that the medium-sized fibres which run in the post-branchial nerves of the Skate may be the homologues of the non-ganglionated splanchnic fibres of the Mammalian spinal accessory nerve.

The Ramus Visceralis.—This, which is the continuation of the main vagus trunk to the heart, stomach, and other viscera, contains fibres which are of two kinds—the medium sized and small medullated. The visceralis ganglion can be traced down the nerve for a distance of about two-thirds of an inch. The cells of it form a well-marked group lying at one side of the nerve, and are multipolar. They do not cause any external prominence. The medium-sized fibres are found commingled with the cells, and almost exclusively at that side of the nerve, becoming few as we pass down the nerve, until, when the nerve cells cease to be found, the medium-sized fibres have practically

[1] *Proc. Roy. Soc.*, 1888.

disappeared; they, in fact, *join the cells of the visceralis ganglion, from which they emerge as small medullated fibres.* The whole of the rest of the nerve and its branches are composed of these finest fibres, whose number is greatly increased below the visceralis ganglion, though the size of the nerve is unaltered, except after its branches form, when, of course, it gradually becomes smaller. The characters of the visceralis ganglion clearly show that it is of the nature of a *vagrant* or splanchnic motor ganglion—in fact, has the same value as a branchial ganglion of the Skate's vagus. This is, perhaps, confirmed by the fact that the fourth vagus-branchial ganglion is confluent with the visceralis ganglion, and it is not at all improbable that this latter ganglion represents, in part, the branchial ganglia of hinder branchial nerves now lost in the Skate. We have evidence that this may be the case from our knowledge of the mode of development of the visceralis branch, which, as shown by Van Wijhe and Beard, behaves like a branchial nerve.

The Ramus Lateralis.—It has previously been shown how the fibres of the roots which are to be distributed to the lateralis become early marked off from the rest. No nerve cells are found in relation to these fibres till at about the origin of the third vagus-branchial. These cells, which form the "lateralis ganglion," can be traced for a short distance down the nerve after it has separated from the visceralis. I have not been able to discover nerve cells in any other part of the lateralis, nor have been able to satisfy myself of the relation they hold to the fibres. The great bulk, though not all, of the fibres in the lateralis are of the large medullated kind—they appear, in fact, *to be exclusively derived from the posterior set of nerve roots.*

It is difficult to be quite sure of the exact morphological value of the lateralis ganglion. At first sight one might be inclined to regard the lateralis and its ganglion as the equivalents of a dorsal sensory somatic nerve root with its stationary ganglion. But we have in the case of lateralis ganglion the important consideration that it is not found on the roots of the nerve like the stationary ganglion of a spinal nerve, but partakes rather of the character of a *vagrant* ganglion. I do not know of an instance in which the somatic sensory ganglion is of a vagrant character,

and am loath to believe that the ganglion now under consideration can be a real exception. Though, of course, the lateralis in function is a somatic sensory nerve, yet the peculiarities of its development, and the other morphological considerations detailed in my former paper, seem to me to render it very doubtful whether it has the character of a somatic sensory nerve root in the ordinary acceptation of the term. I am inclined rather to think that the morphological value assigned to it by Hubrecht,[1] and with which I agreed in my former paper,[2] is the true one. There is nothing in my examination of it to negative this view, whilst, on the other hand, I have not found any great confirmation of the conclusion I have previously arrived at. The fibres of the lateralis, however, are on the average larger than those of a typical spinal sensory nerve root, the former averaging 25 μ, the latter about 20 μ.

Conclusions and Summary.

1. From the preceding description it will be obvious that the nerve cells of the vagus of the Skate are arranged in the following groups:—

(*a*) A small group on the hindermost of the posterior set of roots, which contains fibres passing only into the small dorsal branch. This ganglion is equivalent to a somatic sensory or dorsal root ganglion of a spinal nerve.

(*b*) A group in each branchial branch forming the *branchial ganglia*. These are separate structures in the cases of the first three vagus-branchials, but in the last are confluent with the visceralis ganglion. They are morphologically the *vagrant* ganglia of the splanchnic motor roots of a typical spinal nerve.

(*c*) A second group in each vagus branchial nerve, forming the *prebranchial ganglia*, and found chiefly in the prebranchial branch. These are also *vagrant* in character.

(*d*) A group in the visceralis, forming the *visceralis ganglion*, and morphologically equivalent to *vagrant* ganglia of the splanchnic motor part of a spinal nerve metamer.

(*e*) A similar group in the lateralis, forming the *lateralis ganglion*, and of doubtful homology.

[1] *Loc. cit.*

[2] *Jour. Anat. and Phys.*, 1888, page 387.

2. The vagus of Raia does not contain any non-ganglionated somatic motor fibres. There is only one small fasciculus of ganglionated somatic sensory fibres, viz., the small dorsal branch. The splanchnic motor and probably splanchnic sensory fibres are well marked, and are, as in the case of a typical spinal nerve, divisible into a non-ganglionated portion, which runs chiefly in the post-branchial branches, and a small fibred ganglionated part, which is found in the branchials and visceralis.

3. The vagus nerve of the Skate, therefore, does not contain all the elements of a single perfect spinal nerve metamer.

4. It contains the typical elements of the so-called sympathetic system, viz., splanchnic small medullated fibres, some of which join a proximal set of ganglia, others passing on to a distal set. The proximal set of ganglia are represented by the *branchial* and *visceralis ganglia*, the distal set by the *pre-branchial ganglia* of the Skate's vagus.

5. The conclusions arrived at in my former paper, and some of which are quoted on the first page of the present communication, are in the main confirmed.

EXPLANATION OF PLATES XX., XXI.

Fig. 1 in text on page 441.

Fig. 2. Section across the vagus roots (1 inch obj., × 80 diam. *circ.*). *a.r.*, anterior root fasciculi; *p.r.*, bundle formed by union of posterior set of roots.

Fig. 3. Portion of a transverse section of the posterior set of root fasciculi, showing chiefly large medullated fibres, with a few medium-sized ones ($\frac{1}{8}$ inch obj., × 600 diam. *circ.*).

Fig. 4. Portion of a similar section through the anterior fasciculus of the anterior set of roots, showing chiefly medium medullated fibres, with one or two large ones ($\frac{1}{8}$ inch obj., × 600 diam. *circ.*).

Fig. 5. Portion of a similar section through a part of an anterior root fasciculus, showing chiefly small medullated fibres, with one or two medium-sized ones ($\frac{1}{8}$ inch obj., × 600 diam. *circ.*).

Fig. 6. Transverse section across the main trunk at the level of the commencement of the 3rd branchial branch ($\frac{1}{2}$ inch obj., × 180 diam. *circ.*). *br.g. 3*, third branchial ganglion; *3rd vg.br.*, third vagus-branchial nerve; *v.g.*, visceralis ganglion; *l.g.*, lateralis ganglion; *v.*, visceralis; *l.*, lateralis; *l.m.f.*, large medullated fibres; *m.m.f.*, medium medullated fibres; *s.m.f.*, small medullated fibres.

Fig. 7. Transverse section across the three main branches of the first vagus-branchial ($\frac{1}{2}$ inch obj., × 180 diam. *circ.*). *ph.*, pharyngeal ramus; *pr.br.*, pre-branchial ramus; *pt.br.*, post-branchial ramus; *pr.br.g.*, pre-branchial ganglion.

Fig. 8. Transverse section of the visceralis nerve ($\frac{1}{2}$ inch obj., × 180 diam. *circ.*). *v.g.*, visceralis ganglion; *m.m.f.*, medium medullated fibres; *s.m.f.*, small medullated fibres.

Fig. 9. Two sections of the lateralis nerve. *A*, near its origin; *B*, lower down ($\frac{1}{2}$ inch obj., × 180 diam. *circ.*). *l.g.*, lateralis ganglion; *l.m.f.*, large medullated fibres.

NOTE ON AN AMYLOLYTIC FERMENT FOUND IN THE GASTRIC MUCOUS MEMBRANE OF THE PIG. By Miss GERTRUDE SOUTHALL, *Student of Science*, and Dr JOHN BERRY HAYCRAFT.

WHEN examining the gastric juice of a pig, which had recently been killed, one of us found that it had the property of digesting starch. It contained 0·15 per cent. of acid, calculated as hydrochloric acid. An infusion of the stomach of the same animal was made in normal salt solution. It, too, had ample amylolytic properties, which it lost after the fluid had been raised for a minute or two to the boiling point.

The experiment was repeated with the gastric mucous membrane of another pig. In this case infusions were made both of the cardiac and pyloric portions. Both were capable of digesting starch. In order to obtain quantitative results, a solution of starch, containing 1 gramme of starch to 100 c.c. of water, was prepared.

This was used in all subsequent experiments. The digestive action of infusions of weighed portions of both the pyloric and cardiac mucous membrane was compared with that of infusions made from the same weight of the pancreas of the same animal.

The mixtures containing starch-paste and the infusions to be tested were kept in a water-bath at the temperature of the body. A few drops were periodically withdrawn, and tested with dilute tincture of iodine. During the digestion of the starch the blue iodide of starch was replaced by the brown erythro-dextrine reaction, which itself subsequently disappeared. At this stage it powerfully reduced Fehling solution.

Several of the experiments were performed by Miss Southall in the Mason College Laboratory, and we have to express our thanks to Professor Allen for the kind and valuable assistance which he was ever ready to give to her.

Experiment I.—On the action of gastric juice.

(*a*) Gastric juice, filtered from the rest of the contents of a pig's stomach, added to half its own volume of 1 per cent. starch-paste,

digested it in half an hour. Acidity 0·0365, calculated as hydrochloric acid.

(*b*) Gastric juice of another pig digested a similar quantity of starch in half an hour. Acidity, calculated as hydrochloric acid, 0·1095 per cent.

Experiment II.—An experiment in which the digestive properties of the gastric mucous membrane were compared with those of the pancreas.

In each case one volume of an infusion, made from the same weights of the glandular structure to be compared, was added to two volumes of starch-paste.

(*a*) The pancreatic infusion digested the starch within fifteen minutes.

(*b*) The cardiac infusion digested the starch in less time than fifty minutes.

(*c*) The pyloric infusion digested it in less than thirty minutes.

It is seen then that, although not so powerful as the pancreas, yet the gastric mucous membrane has a well-marked digestive action on starch, especially, perhaps, the pyloric portion. The experiment was repeated with similar results.

Experiment III.—To determine whether the ferment can act in the presence of free hydrochloric acid.

(*a*) An infusion of the cardiac mucous membrane diluted with one volume of water, and added to another volume of starch extract, digested the latter in less than fifteen minutes. Another portion of the same infusion, added to the starch and to one volume of 0·1 per cent. hydrochloric acid, did not digest it at all. In this case the ferment was unable to act in a 0·03 per cent. solution of the acid.

(*b*) An infusion of the pyloric mucous membrane, diluted in one case with water and in another case with 0·1 per cent. hydrochloric acid, digested the starch, in the first case in less than a quarter of an hour, and did not digest it at all in the acid solution.

This experiment was repeated with a weaker acid solution than the above, and showed that the digestive action was arrested in an acid fluid containing as little as 0·01 per cent. of free hydrochloric acid.

It is not difficult, however, to account for the digestive action of the acid gastric juice itself, for it is probable that free hydrochloric acid is generally, or very frequently, absent from the stomach of the pig, the acidity being due to organic acids; and it is well known that these latter acids do not affect the digestive action of amylolytic ferments in so material a way.

From two of the above samples of gastric juice, by far the larger amount of acid was readily removable by ether, and probably there was little or no hydrochloric acid in the residue.

Many parts of the pig are said to slightly digest starch. In the case of the gastric mucous membrane this power is well

marked, and is probably a factor of some importance in digestion.

While in the pig the gastric juice is in the majority of cases an active starch digester, yet we have come across two or three samples which were absolutely inert.

Each of five infusions made from the gastric mucous membranes of five pigs killed in the slaughter-house in Birmingham was a strong starch digester. Among a similar number of infusions made from Edinburgh pigs, it was an exception to find one with any action at all. The difference was perhaps due to these having been killed in different phases of digestion. It is not impossible that an additional cause may have been the use of a different diet for fattening.

EXPERIMENTS IN CRANIO-CEREBRAL TOPOGRAPHY.[1] By WILLIAM ANDERSON and GEORGE HENRY MAKINS.

IT appears almost necessary to apologise for bringing forward a new contribution to a subject so recently and so largely discussed as the surface localisation of the cerebral convolutions. It was, indeed, only after a very careful study and comparison of the important labours of our predecessors that we were induced to undertake a further series of investigations, the objects of which were as follows:—

1. To map out the latitude and longitude of the cranium by means of a few simple lines running between points that are capable of precise definition upon the scalp, and so adjusted that their position with relation to the parts of the brain surface should not be materially affected by ordinary variations in the form and dimensions of the skull.

2. To register, in as many subjects as possible, the relations to the cranial lines above mentioned of the principal brain-sulci, in order to define the normal range of variation in the position of these, and establish a series of surface points which shall be axial for all the known or probable situations of certain points in the course of the fissures.

Our observations have been divided into three groups. A preliminary series of examinations were conducted with a view to gain certain approximate data as to the relations of the three principal brain fissures to the cranial walls. Upon the indications so obtained were founded a second and larger set of investigations, mainly guided by experimental punctures made at certain test points upon the scalp; and, lastly, a number of adult crania of different types, but free from abnormalities of form or development, were submitted to admeasurements with a view to determine the range of variation of the principal sutures, eminences, and ridges in their relation to each other and to certain standard lines drawn upon the surface of the skull.

[1] Read before the Anatomical Society of Great Britain and Ireland, February 1889.

The first series included six subjects between the ages of 20 and 50. In each observation one-half of the vault of the cranium was removed, exposing nearly the whole of the outer aspect of the corresponding hemisphere with its membranous investments. The dura mater was divided sufficiently to allow the course of the fissures of Rolando and Sylvius and of the external parieto-occipital fissure to be accurately determined. This effected and the membrane sutured, the outlines of the sulci were marked upon its surface with a strong coloured mucilage. The detached portion of the skull was then carefully replaced, and the head was turned over in such a manner as to bring the mucilaginous tracing into contact with the inner aspect of the opposed bone. The segment of the calvaria was again removed, and along the sulcus-lines printed upon its inner table a number of holes were drilled through the whole thickness of the bone at right angles to its surface, and note was taken of the relation of these punctures, as seen from the exterior, to the various sutures and eminences.

The indications so obtained, when united upon a skull of average dimensions, enabled us to draw a brain-plan which might be regarded as sufficiently near to the truth to serve as a basis for further experiments. Certain points were then fixed tentatively, as corresponding to the two extremities of the fissure of Rolando, the "commencement," middle, and termination of the fissure of Sylvius, and the upper end of the external parieto-occipital fissure. Finally, three standard lines were devised as a guide to the localisation of these points upon the scalp. The lines in question were then marked upon the subject, the skull drilled at certain spots through punctures in the scalp in each of the lines, and through the several apertures long pins were introduced into the brain substance at right angles to the surface. On exposure of the hemispheres by removal of the skull-cap we now had a number of pins marking the parts of the brain immediately subjacent to the selected "chart" points on the scalp, and it was easy to take a note of the exact relationship between the brain punctures and certain points in the fissures under investigation.

Experiments upon this plan have been made in twenty subjects; three children, aged 2½, 8, and 14; three women, aged 16,

24, and 28; and fourteen men, whose ages ranged between 19 and 68; both hemispheres being examined in each instance. Assuming that the experimental punctures had been made with due care and the inter-relation between the chart points and fissure points correctly registered upon a suitable diagram in each case, the union of the fissure points upon a single diagram would give for each spot under consideration a dotted area indi-

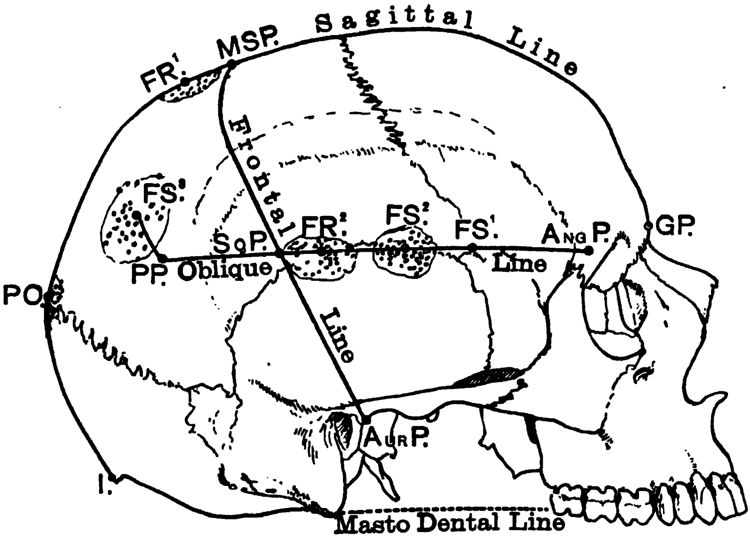


FIG. 1.—Drawing of a skull, showing variations of position in bifurcation and termination of fissure of Sylvius (figs. 2 and 3); of two extremities of the fissure of Rolando (FR¹ and FR²); and of the parieto-occipital fissure (PO). GP, Glabellar point; I, Inion; MSP, Mid. sagittal point; Aur. P, Pre-auricular point; Ang. P, Angular point; Sq. P, Squamosal point; PP, Parietal point.

cating the range of variation of its position; and the most central point in this area might be accepted as the most suitable place for the application of the pin of the trephine.

The guiding lines devised for this localisation of the fissure points were three in number:—one, sagittal and mesial, extending from the glabella at a point midway between the highest points in the supraorbital arches to the external occipital protuberance; the second, nearly frontal in direction, running from the mid-point of the sagittal line to the depression immediately in front of the tragus, at the level of the upper border of the meatus; the third

passing obliquely from the most prominent point of the external angular process, at the level of the superior border of the orbit, to the junction of the middle and lower thirds of the frontal line, and prolonged for about an inch and a half behind this. In the adult it usually runs a little above the highest point of the squamous suture, and nearly parallel to a line drawn from the edges of the upper teeth to the tip of the mastoid process. The lines we have designated respectively by the names of "sagittal," "frontal," and "squamosal," and the points corresponding to their extremities, as glabellar, mid-sagittal, inial, pre-auricular, angular, squamosal, and parietal (see diagram). It will be noticed that the position and direction of the frontal and squamosal lines shift in association with variations in the form and size of the skull. No base line is employed.

TABLE I.—*Scalp Measurements of Sagittal, Frontal, and Squamosal Line in 20 Subjects.*

No.	Sex.	Age.	Sagittal Line.	Frontal Line.	Squamosal Line.	No.	Sex.	Age.	Sagittal Line.	Frontal Line.	Squamosal Line.
1	M.	36	$13\frac{1}{2}$	$6\frac{7}{16}$	$3\frac{1}{4}$	11	M.	38	$13\frac{1}{4}$	$6\frac{7}{8}$	3
2	M.	25	$12\frac{3}{8}$	$6\frac{11}{16}$	3	12	M.	38	$13\frac{1}{2}$	$6\frac{3}{4}$	3
3	M.	57	$12\frac{3}{4}$	$6\frac{3}{4}$	$3\frac{1}{4}$	13	M.	8	$12\frac{3}{4}$	$6\frac{5}{8}$	$2\frac{1}{2}$
4	M.	39	$12\frac{7}{8}$	$6\frac{5}{8}$	3	14	M.	53	14	$7\frac{1}{2}$	$3\frac{1}{2}$
5	M.	30	$13\frac{1}{2}$	$6\frac{3}{8}$	3	15	M.	19	$13\frac{1}{2}$	7	$2\frac{3}{4}$
6	M.	51	14	$6\frac{7}{8}$	4	16	M.	68	$13\frac{1}{2}$	$6\frac{5}{8}$	...
7	F.	24	$13\frac{1}{2}$	7	$3\frac{1}{2}$	17	F.	28	$12\frac{1}{4}$	$6\frac{3}{8}$	$2\frac{3}{4}$
8	F.	16	$12\frac{7}{8}$	$6\frac{1}{2}$	3	18	M.	$2\frac{1}{2}$	$11\frac{1}{8}$	$5\frac{7}{8}$	$2\frac{1}{2}$
9	M.	14	12	$6\frac{3}{8}$	3	19	M.	28	$13\frac{1}{2}$	...	$3\frac{1}{2}$
10	M.	34	13	$6\frac{7}{8}$	3	20	M.	24	$13\frac{3}{4}$	$6\frac{15}{16}$	3

The third set of investigations, undertaken in order to test the value of the sutures and eminences of the cranium as indications to the position of the brain regions, were carried out upon thirty skulls. The measurements recorded were as follows:—

1. The length of the sagittal line from the glabella to the external occipital protuberance (inion). This served as the denominator of a fraction, of which 2 and 3 were the numerators.

2. The distance from the glabella to the bregma.

3. The distance from the external occipital protuberance to the highest point of the lambdoid suture.

4. The length of the half frontal line, from the mid-sagittal

point to the pre-auricular point. This, in turn, served as denominator for fractions, of which 5 and 6 were the numerators.

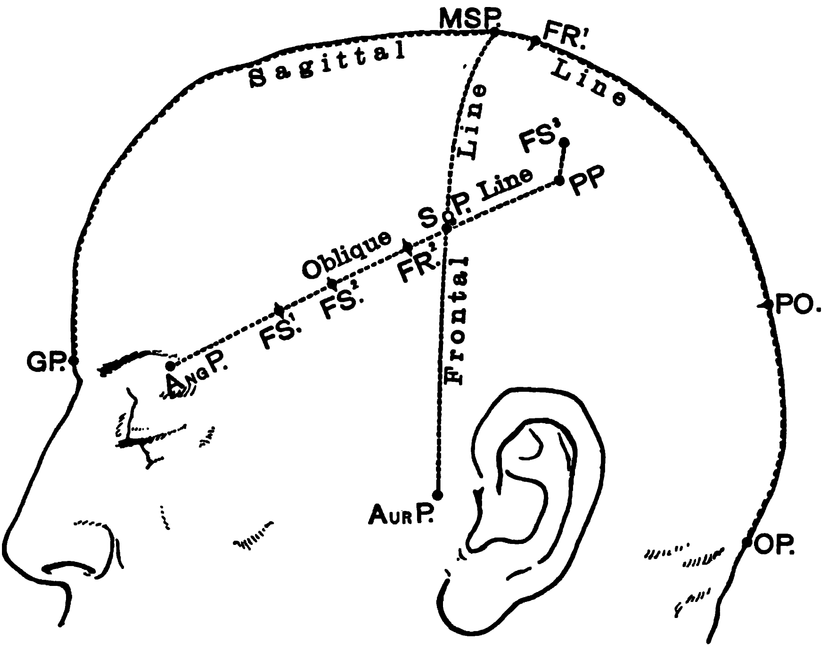


FIG. 2.—Cranio-Cerebral guiding lines, traced upon a Cast of Prof. Cunningham's (from a photograph). GP, Glabellar point; glabella opposite superior border of orbit. IP, Inial point, at external occipital protuberance. MSP, Mid-sagittal point; midway between GP and IP. Ang. P, Angular point; external angular process opposite upper border of orbit. Sq. P, Squamosal point; intersection of oblique and frontal lines at junction of middle and lower thirds of latter. PP, Parietal point; termination of oblique line, equidistant with FS^2 from squamosal point. Aur. P, Pre-auricular point; depression in front of tragus, at level of upper border of external auditory meatus. FS^1, "Commencement" of fissure of Sylvius, $\frac{5}{12}$ths of distance from Ang. P to Sq. P. FS^2, Bifurcation of fissure of Sylvius, $\frac{7}{12}$ths of distance from Ang. P to Sq. S. FS^3, Termination of fissure of Sylvius, $\frac{1}{2}$ an inch above PP, in a direction parallel to frontal line. FR^1, Upper extremity of fissure of Rolando carried to sagittal line in direction of fissure, $\frac{3}{8}$ths of an inch behind mid-sagittal point. FR^2, Lower extremity of fissure of Rolando carried to oblique line in direction of fissure, $\frac{3}{8}$ths of an inch in front of squamosal point. PO, External parieto-occipital fissure, carried to sagittal line in direction of fissure, $\frac{7}{12}$ths of distance from MSP to OP.

5. The distance (in the course of the frontal line) from the pre-auricular point to the highest point of the squamous suture.

6. The distance from the pre-auricular point to the superior and inferior temporal ridges, where these are crossed by the frontal line.

7. The distance of the centre of the parietal eminence from the frontal line.

8. The length of a line passing through the centre of the parietal eminence from the pre-auricular point to the sagittal line. This formed the denominator, for a fraction of which 9 was the numerator.

9. The distance of the centre of the parietal eminence from the pre-auricular point in this line.

10. The distance of the centre of the frontal eminence from the supraorbital arch in a vertical line, and from the sagittal line in the horizontal direction.

11. The distance of the external occipital protuberance to the posterior border of the foramen magnum.

12. The width of the mastoid process at its base.

The results are tabulated at the end of the paper. The more important practical facts demonstrated by our experiments up to the present time are as follows:—

1. The cranial sutures, ridges, and eminences accepted as a guide to the convolutions and sulci, are sufficiently variable as to their position in relation to each other and to the cranial walls as a whole to introduce an undesirable source of fallacy in brain surgery. Thus the summit of the parietal eminence, which is usually about midway in a line passing through between the pre-auricular point and the sagittal suture, has a range of variation of nearly half an inch in the vertical and an inch in the horizontal direction (after correction has been made for the varying dimensions of the skulls). The distance of the bregma from the glabella, which averages about two-fifths of the length of the sagittal line, has a corrected range of variation of a little over half an inch. The distance of the apex of the lambdoid suture from the external occipital protuberance, usually a little more than one-fifth of the length of the sagittal line, varies to the extent of seven-eighths of an inch. The squamous suture and the temporal ridges are equally uncertain as to place, the former varying to the extent of three-fourths of an inch, the latter to one inch, in the dis-

tance from the pre-auricular point in the frontal line. The level of the spheno-parietal suture was no less variable. The frontal eminence, like the parietal boss, may be very imperfectly marked, and hence difficult to localise, and exhibits similar variations of position, both in the vertical and horizontal direction, which do not appear to be related to corresponding alterations in the conformation of the subjacent portion of the brain; lastly, the mastoid process not only presents considerable differences in size (three-fourths of an inch in width at its base) in different crania, and a complete absence of relation to cerebral development, but in the living subject is usually obscured as to its posterior limits by the insertion of the sterno-mastoid muscle.

The eminences most easy of definition through the scalp are the glabella, the external angular process, and the external occipital protuberance; and although, like the rest, these are subject to irregularities of position, the variations are too small to interfere seriously with the value of the points as surgical landmarks.

2. The relations of the cerebral convolutions and sulci to the cranial surface and to each other vary within rather wide limits in different subjects, and even upon the two sides of the same head; it is hence dangerous to claim for any portion of the brain a fixed and invariable point of localisation. All that is possible for the anatomist to do is to indicate upon the scalp an easily-defined spot which shall hold a central position with regard to all the probable variations of the brain locality under consideration, and this we have made the chief object of our labours.[1]

3. Most if not the whole of the fissures and convolutions, although sufficiently constant in character and position to permit easy recognition, are often very capricious in their course. For example, the fissure of Rolando, with its limiting convolutions,

[1] Attention has already been directed in this *Journal* to variations in position of some of the cerebral fissures, by Professor Turner, vol. viii., 1873, and in his Report of the Human Crania in the "Challenger" Reports (part xxix., 1884) he showed how variations in the cranial bones rendered it difficult to lay down fixed rules for the determination of the relation of the cerebral convolutions and fissures to the surface of the head. Mr A. W. Hare also, in his paper in this *Journal* (Jan. 1884, vol. xviii.), treats on the variability more especially of the fissure of Rolando and the parieto-occipital fissure.

may run from end to end without material deviation from the most direct lines between the two points, or it may, especially in its upper third, describe curves of such strength that an inch trephine applied over the line joining the two extremities of the curve might fail to expose the sulcus. The diagrams show a few tracings taken from a series of subjects, without selection, to illustrate this point. Again, the posterior portion of the so-called horizontal limb of the fissure of Sylvius, which mainly determines the form and position of the supra-marginal gyrus, varies so much in its course and place of termination, that it is not possible to ensure its exposure within the circumference of a trephine of an inch in diameter.

4. The system of charting described has been found to hold good, so far as our experiments go, for women and children as well as for adult males. It is hardly necessary, however, to say that the precise influence of age and sex upon localisation cannot be determined without greatly extended observations.

These facts being premised, the positions of the principal fissures may be recorded as follows:—

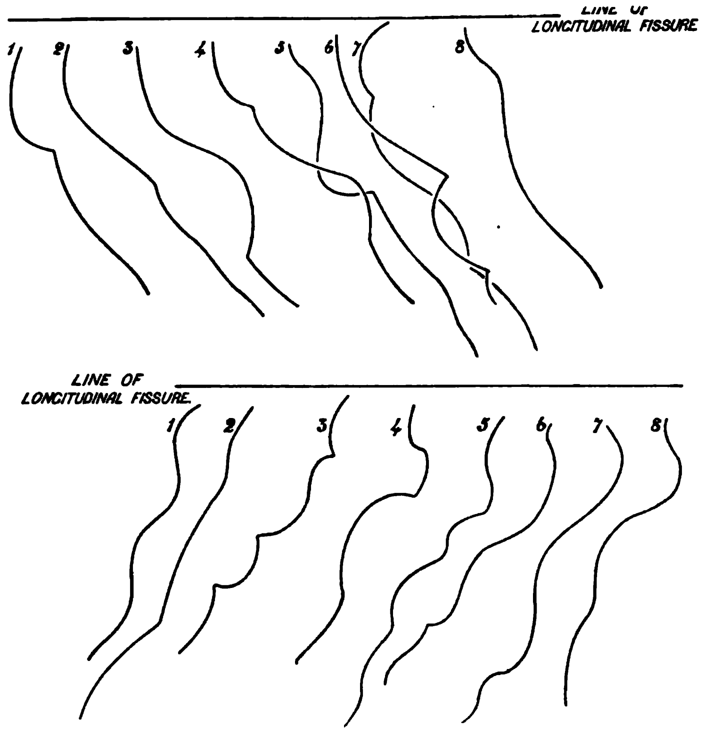
1. *Fissure of Rolando.*—The upper extremity, carried for convenience of admeasurement as far as the longitudinal fissure (in line of the sulcus), was found to lie in all cases between the mid-sagittal point and a point three-quarters of an inch behind it. Its distance behind the mid-sagittal point, however, bore no constant relation to the length of the sagittal line, and hence the central spot for the application of the trephine may be most safely fixed at three-eighths of an inch behind the mid-sagittal point.

The superior connecting gyrus between the precentral and post-central (ascending frontal and parietal) convolutions occasionally appears only on the mesial surface of the hemisphere—in this case the fissure of Rolando actually reaches the longitudinal fissure.

The lower end of the sulcus, carried into the fissure of Sylvius, lies in the squamosal line between the junction of this line with the frontal line (squamosal point), and three-fourths of an inch in front of this. The centre of the trephine may hence be applied, in the squamosal line, three-eighths of an inch in front of the squamosal point. In four instances the sulcus really joined the horizontal limb of the Sylvian fissure.

The angle formed, with the upper border of the hemisphere, by a line connecting the two extremities of the fissure of Rolando, in eight cases (sixteen fissures) was found to range between 55° and 70°, in twelve falling between 60° and 65°.[1] It is, however, doubtful whether this observation can be turned to any practical account.

The *course* of the fissure is extremely capricious, and tracings



taken from opposite hemispheres often differ considerably from each other (see diagram). A strong curve with a backward con-

[1] It is scarcely possible to ensure scientific accuracy in measuring angles upon an irregularly-curved surface, but a sufficient degree of correctness for practical purposes may be attained. Serviceable goniometers for the admeasurement of the fissure of Rolando may be made from segments of the vault of a thin cranium, cut on either side of the median line of the frontal and anterior parietal region, and terminating behind by a frontal section at the level of the mid-sagittal point. The outer surface of this may then be graduated as far as necessary (between 50° and 90°). For multiplied observations three sets of goniometers, representing crania of different dimensions (small, medium, and large), should be provided.

vexity is not unfrequently met with in the upper third, and a second smaller curve in the opposite direction may sometimes be found near the lower extremity of the sulcus.

2. *Fissure of Sylvius.*—The place at which the frontal and temporo-sphenoidal lobes appear to separate when seen from the lateral aspect of the brain—the so-called "commencement of the fissure of Sylvius"—can scarcely, from its very nature, be fixed with complete exactness, but it may be computed with sufficient accuracy for all practical purposes. It was found to lie in the squamosal line beween $1\frac{1}{8}$ and $1\frac{1}{2}$ inch behind the external angular process, or about $\frac{5}{12}$ths of the distance between the point and the frontal line.

The bifurcation of the fissure lies in the squamosal line at a point from $1\frac{1}{2}$ to 2 inches behind the external angular process, or at $\frac{7}{12}$ths between this process and the frontal line. The course of the horizontal limb from the bifurcation to the frontal line corresponds closely to the squamosal line and a continuation of this backwards for an equal distance behind the frontal line (to parietal point in diagram), it then turns upwards for about half an inch in a direction parallel to the frontal line. The mode of termination of the fissure is, however, so uncertain, that a circle of an inch in diameter failed to cover all the variations in the twenty subjects examined by us. The parietal eminence is nearly always closely related to the point in question.

3. The *external parieto-occipital fissure* joins the longitudinal fissure at a point averaging $\frac{7}{12}$ths of the distance measured from the mid-sagittal point to the external occipital protuberance, and lies near to the apex of the lambdoid suture.

In operations in the neighbourhood of the longitudinal fissure, it is of course necessary to take into consideration the width of the superior longitudinal sinus and its frequent deviation towards the right side in the posterior half of its course.

An endeavour was made to ascertain the average positions of the superior and inferior frontal fissures, but these were found to be so irregular in their course as to baffle all attempts to secure indications of any value.

TABLE II.

Table II.—*Measurements of Skulls.*

No.	In Sagittal Line.				In Frontal Line.				In Oblique Line.					
	Sagittal Line.	Bregma from Glabella.	Lambda from Occipital Protuberance.	Foramen Magnum from Occipital Protuberance.	Frontal Line.	From Pre-auricular Point. Squamous Suture.	From Pre-auricular Point. Lower Temporal Ridge.	From Pre-auricular Point. Upper Temporal Ridge.	Oblique Line from Pre-auricular Point to Sagittal Line crossing Parietal Eminence.	Parietal Eminence from Pre-auric Point.	Parietal Eminence from Frontal Line.	Frontal Eminence from margin of Orbit.	Frontal Eminence from Median Line.	Width of Mastoid Process.
1	11¾	4½	2½	1¾	6	1¾	2¾	3⅛	6⅛	3	⅞+	Indefinite.	Indefinite.	¾+
2	13¼	5	3	2	6¾	2	3¼	4¼	6⅞	3⅝	⅞	1⅜	1⅛	1⅛+
3	11½	4⅜	2⅝	2	6⅛	2	2⅞	3⅝	Indefinite.	Indefinite.	Ill marked	1⅜	1⅜	1
4	12½	5	2⅝	1⅞	6⅝	? 2	3¼	3¾	6⅝+	3⅝	1	1⅜	1¼	⅞
5	13½	5	3	2	6⅝	1⅞	3⅝	4	6⅞	3⅝	¾	1¼	1¼	1⅛
6	12	4¾	2¼	1⅞	6⅝	1⅝	3¼	3¾	6⅝	3⅝	¾	1½	1¼	¾
7	12½	4¾	2½	2⅜	6½	2	3⅜	4⅜	7	3⅝	⅞	1¼ {Indistinct.}	1⅜	¾
8	12½	4¾	2⅛	...	6¾	2¼	...	...	7	3¼	1	1¼	1½	...
9	12	4⅝	2⅝	2¼	6⅝	2¼	3⅛	4¼	6⅝	3⅛	1	1⅜	1¼	...
10	13⅜	5⅝	2⅞	2	7	2	4⅛	5⅝	7⅛	3⅛	⅞	1⅜	1	...
11	13¼	5¼	3	...	7	2	3¼	3¾	7⅛	3¼	1	1⅜	1¼	...
12	12⅝	4⅝	3	1⅛	6½	1⅞	Indefinite.	Indefinite.	6⅛	3⅛	⅝	1¼	⅞	...
13	13	5⅛	2⅝	2	7	2¼	3¼	3¾	7⅜	3⅛	¾	1⅜	1	1⅜
14	13	4¾	3	1⅛	6⅛	1⅞	3⅜	4⅛	6¾	3⅛	⅞	1⅜	1⅛	1¼
15	13¼	4¾	3¼	1¼	6⅝	2¼	3⅝	3⅝	6¾	3⅝	⅞	1⅜	⅞	1⅛
16	12¼	4¾	2⅛	2⅛	6⅝	1⅞	3	3¼	6¼	3⅞	⅞	1¼	1⅛	⅝
17	12¾	4¾	3	1⅛	6⅝	2¼	3	3⅝	6⅝	3⅛	¾	1¼	1⅜	1
18	11¾	4⅝	1⅝	1¾	6⅞	1¼	3	3¼	6⅝	3¼	¾	1⅛	1⅜	⅞
19	11¾	4⅛	2⅛	1⅞	5¾	1⅞	2⅞	3¼	6¼	3⅜	⅝	1⅛	1⅜	⅞+
20	12⅜	4⅝	3	1⅛	6¾	1⅞	3⅝	3¾	7	3⅝	1	1⅜	1	⅞−
21	12¾	5	2⅝	1⅞	6¾	2	3⅝	4	7⅛	3⅝	⅝	Indefinite.	Indefinite.	1⅛
22	12⅝	4⅛	2⅞	1⅝	6	1⅞	2⅞	3¼	6⅛	3⅛	1⅛	1³⁄₁₆	1¹⁄₁₆	1
23	13	5⅛	2⅝	1⅞	6⅝	1⅞	3⅝	3⅞	6⅞	3⅛	1	1¼	1⅛	⅞
24	12	4⅞	2⅝	2⅛	6¼	1⅞	3¼	3⅞	6⅝	3¼	⅞	1⅜	1⅛	⅞
25	12	4¾	2⅛	1⅝	6¾	2⅛	3⅛	3½	Indefinite.	Indefinite.	Indefinite.	1⅜	1⅛	⅞
26	13	5	2⅝	1⅞	6⅝	1⅝	2⅞	Indefinite.	Indefinite.	Indefinite.	Indefinite.	Indefinite.	Indefinite.	⅞
27	12	4¾	2⅛	2	6¼	1⅞	3¼	Indefinite.	6⅛	3⅛	1⅛	1⅛	1	1⅛
28	11¾	4¾	2⅛	2	6¼	2	3⅝	4⅛	6⅝	3⅛	1¼	1¼	Indefinite.	1⅛
29	11⅛	4¾	2	1⅞	6¼	1⅝	2⅝	3¼	6⅝	3⅛	1¼	1	1	⅞
30	11⅛	4⅜	2½	1¾	6¼	1⅞	3	3⅝	(r) 6¼ (l) 6⅞	(r) 3⅝ (l) 3¼	(r) 1⅛ (l) 1⅛	1⅜+	1⅜	⅝

The marks + and – indicate that the lengths recorded were exceeded or the reverse to the extent of a small fraction of an inch.

ADDITIONAL OBSERVATIONS ON THE STOMACH IN THE ZIPHIOID AND DELPHINOID WHALES.

By Professor Sir WM. TURNER, M.B., LL.D., F.R.S.

FROM time to time I have communicated to this *Journal*[1] observations on the stomach in the Cetacea, more especially in certain species of the Delphinidæ and Ziphiinæ. Since the date of my last paper, October 1885, I have had opportunities of making some additional dissections of the stomach in certain species belonging to these families, and I propose in this communication to speak of the stomach in *Micropteron* (*Mesoplodon*) *bidens*, *Hyperoodon rostratus*, *Phocæna communis*, *Delphinus delphis*, *Delphinus* (*Lagenorhynchus*) *albirostris*, *Monodon monoceros*, *Delphinapterus leucas*.

ZIPHIINÆ.

Stomach of Micropteron bidens.—In my account of the specimen of Sowerby's whale captured in Shetland in 1885, I described the stomach of the animal, and discussed some points bearing on the morphology of that organ in the Cetacea generally. I came to the conclusion (*a*) that in Sowerby's whale the stomach was divided into a greater number of compartments than in any other known cetacean; (*b*) that the first gastric compartment, both in this and other Ziphioid whales, was not homologous with the œsophageal or 1st compartment of the stomach in the Dolphins; (*c*) that it was a true digestive chamber, and was homologous with the 2nd gastric compartment in the Dolphins; (*d*) that the œsophageal compartment of the stomach in the Delphinidæ is wanting in the Ziphioid whales.

In October 1888, I obtained another specimen of Sowerby's whale, which had been stranded in Dalgety Bay, on the north side of the Firth of Forth.[2] The stomach of this animal was

[1] "A Contribution to the Anatomy of the Pilot Whale (*Globiocephalus Svineval*)" (Nov. 1867, vol. ii.); "Further Observations on the Stomach in the Cetacea" (Nov. 1868, vol. iii.); "Anatomy of Sowerby's Whale" (Oct. 1885).

[2] I have given an account of the dimensions and external characters of this specimen in the *Proc. Roy. Phys. Soc. Edin.*, Dec. 19, 1888.

removed and inflated, and when in the distended condition a careful drawing was made of it (fig. 1). It was then dried, and its compartments subsequently opened into, so as to be preserved as a Museum specimen. It may be regarded as consisting of three chief divisions—proximal, intermediate, and distal.

The proximal or cardiac division (1), before it had somewhat shrunk in the act of drying, was 21 inches long and between 8 and 9 inches in its greatest transverse diameter. It

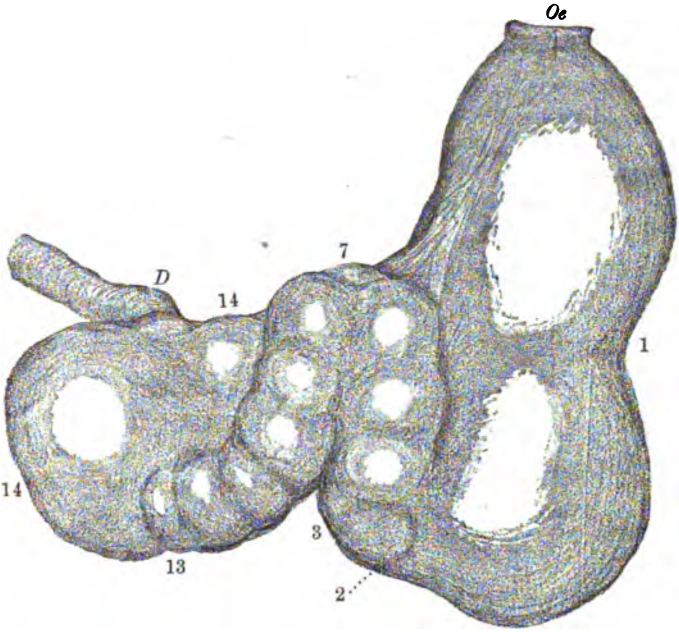


FIG. 1.—Ventral surface of stomach of *Micropteron bidens*. *Oe*, œsophagus; *D*, duodenum. The numerals refer to the several compartments of the stomach. 2 points approximately to the 2nd compartment not visible in the figure. This and the following figures are from drawings of the stomach, by my pupil, Mr Harry G. Melville.

formed the left or cardiac bag of the stomach, and had about the middle of its surface an almost circular constriction, which divided it into two dilated parts nearly equal in size. The position of the constriction was marked in the interior by a projecting fold of mucous membrane, not so deep as to act as a valve, and permitting free communication between the two dilatations. At its anterior end it had a free communication

with the œsophagus. At its posterior end it opened by a short funnel-shaped passage into the 1st compartment of the intermediate division of the stomach, and a strong valvular fold of mucous membrane was situated at the opening. It possessed thicker walls than any of the other gastric compartments, principally owing to the thick folds of its mucous lining.

The intermediate division consisted of twelve subglobular compartments (2–13), varying in size from a small to a large orange. They were arranged so as to form a Λ-shaped figure with the apex directed forwards. The proximal limb of the Λ, which lay next to the cardiac division, consisted of five compartments. Another compartment was situated at the apex where the proximal and distal limbs became continuous with each other, and the distal limb was subdivided into six compartments. The separation between the different compartments was marked on the surface of the organ by a series of constrictions, which passed more or less circularly around the stomach; whilst internally a broad valve-like fold of mucous membrane projected both from the upper and lower walls, but did not meet in the axis of the lumen. An aperture of communication was therefore between each compartment and that on each side of it; the arrangement being somewhat like that of the foramen ovale in the auricular septum of the heart of the human fœtus. But further, I may state that in more than one of the globular compartments of this division a fold of mucous membrane projected from a part of the wall into the lumen, which, if it had been deeper and had extended farther round the wall, would have still further subdivided this portion of the stomach. The whole of the compartments of the intermediate division were visible on the ventral surface of the stomach, except that (2) which opened directly into the cardiac division (1), was placed on the dorsal aspect of that division a little in front of its posterior end, and is not seen therefore in figure 1, which gives the ventral aspect of the stomach.

The distal or pyloric division of the stomach (14) before being dried was 11 inches in its long diameter from right to left, and 9 inches in its antero-posterior diameter. It was marked by a circular constriction on the surface, with which a shallow ring-like fold of mucous membrane corresponded internally, so that

it possessed indications of a separation into two chambers, but as the communication between them was so wide they could not be regarded as distinct compartments. Of these two chambers the right was the larger, was almost globular in shape, and formed the right or pyloric end of the stomach. The left or smaller chamber was wedged in between the distal limb of the intermediate division and the proximal division of the stomach. Both the last compartment of the intermediate division and the duodenum communicated with the larger of these two chambers, so that the smaller chamber was as it were a wide diverticulum from the larger. The duodenum sprang abruptly from the posterior wall of the larger chamber, and its opening into that chamber was immediately opposite the opening of communication with the last compartment of the intermediate division. Both these openings were immediately to the right of the ring-like fold of mucous membrane which indicated the division of 14 into two chambers, and each opening was nearly in the centre of a strong and almost circular valve-like fold of mucous membrane.

The Duodenum, slightly dilated, was 2 inches in breadth at its commencement, and then almost immediately became a cylindrical tube. Its dilated end was prolonged as a short *cul-de-sac* about an inch to the left of its pyloric opening. The mucous lining of the *cul-de-sac* and of the anterior wall of the duodenum opposite the pyloric orifice was smooth. Immediately beyond the opening it was thrown into valvulæ conniventes, which were arranged circularly around the wall, and the intervals between them were occupied by reticulating folds of the mucous membrane.

This description of the stomach of Sowerby's whale differs in several particulars from my account of the stomach of the specimen (A) dissected in 1885. I have recognised in this more recent specimen (B) a subdivision of the organ into no fewer than 14 compartments, whilst in the previous example only 10 were described. The demarcation between the compartments was marked both by constrictions on the surface and by valve-like apertures of communication internally. In both examples the proximal and distal divisions corresponded respectively with each other, and the difference between the two

stomachs was in the number of compartments in the intermediate or Δ-shaped division. In A only eight were recognised, whilst in B as many as twelve were seen. It is possible that the difference in the number recognised may have been due to B having had a greater number of subdivisions than A; but it may also be due to B having been examined under more favourable conditions, both as regards the facilities for handling it and its comparative freshness; for, in the flaccid state which A was in when it reached me, it is possible that some of the smaller compartments of the Δ-shaped division may have been overlooked. The similarity in form and in the mode of internal communication of the twelve compartments of the Δ-shaped division leads me to regard them as homologous with each other, and as presenting a remarkable example of repetition of structure, so that I have grouped them together as forming a division of the stomach intermediate to the proximal and distal portions. But I would also point out that both the proximal and distal divisions, with their surface constrictions and projecting folds internally, exhibited a tendency to incomplete subdivision into smaller chambers, although the internal folds were not sufficiently deep to justify one in regarding these chambers as separate compartments.

In my description of A, I stated that the pancreatic duct was "about as large as the human femoral artery," and opened into the duodenum about 5 inches from the pylorus. From my more recent dissections I am of opinion that this large duct was the conjoined pancreatico-hepatic duct. My imperfect interpretation of its nature on that occasion, its connection with the liver having previously been cut through, was due to its being surrounded by the lobules of the pancreas at its duodenal end, which I am now satisfied is the rule in the Cetacea, so that it seemed to be the duct of the pancreas.

Stomach of Hyperoodon rostratus.—In my original account of the stomach of Sowerby's whale, I compared it with the published descriptions by John Hunter, Dr Jacob, Vrolik, and Eschricht of the stomach of Hyperoodon and with an inflated and dried specimen of the latter animal in the University Museum. A fresh specimen of the stomach of Hyperoodon was not at that time in my possession, but having preserved the

viscera of a young male captured at Dunbar in November 1885,[1] I have subsequently been able to examine the recent stomach of this animal, and to make a comparison between it and that of Sowerby's whale.

The Œsophagus was 4 inches in its transverse diameter a few inches in front of the stomach, but at its gastric end it was constricted to about an inch. Its entrance to the stomach was marked by an almost circular fold of mucous membrane, and its mucous lining presented a strong contrast in appearance to that of the cardiac division of the stomach.

The Stomach itself consisted of seven distinct compartments, arranged so as to form a proximal, an intermediate, and a distal division.

The proximal or cardiac division (1), somewhat pyriform in shape and directed backwards, was 21 inches long and 8¾ inches in greatest breadth. It was covered both ventrally and laterally by peritoneum; the spleen was attached to its left surface by a broad gastro-splenic omentum, and upon its posterior end a broad omental fold was prolonged backwards for upwards of 2 feet. At its anterior end it opened into the œsophagus. There was no constriction on its surface to indicate a partial division into two chambers. When this compartment was everted its mucous lining was seen to be elevated into strong folds similar to those which I described in Sowerby's Whale as containing numerous glands of the cardiac type of secreting glands.

The proximal was succeeded by the intermediate division, which consisted of five subglobular compartments (2–6), varying in size from a fœtal head to that of an adult. They were arranged so as to form a Δ-shaped figure, with the apex directed forwards. The two smallest compartments (2, 3) formed the ascending limb, the apex of the Δ consisted of compartment 4, about the size of an adult head, whilst the descending limb consisted of compartments 5 and 6, which were somewhat bigger than 4. All these compartments were seen on the ventral aspect of the stomach; they were differentiated from each other by circular constrictions, and were covered on the ventral sur-

[1] I gave an account of the external characters of this animal in *Proc. Phys. Soc. Edin.*, vol. ix., 1886.

face by peritoneum, a broad omental fold of which projected backwards from the posterior border of 6. The first compartment (2) of the intermediate division communicated with the right aspect of the proximal division by an opening situated about 15 inches from its œsophageal end, and therefore comparatively near to the posterior end of the proximal division. The several compartments of the intermediate division communicated successively with each other by openings in the

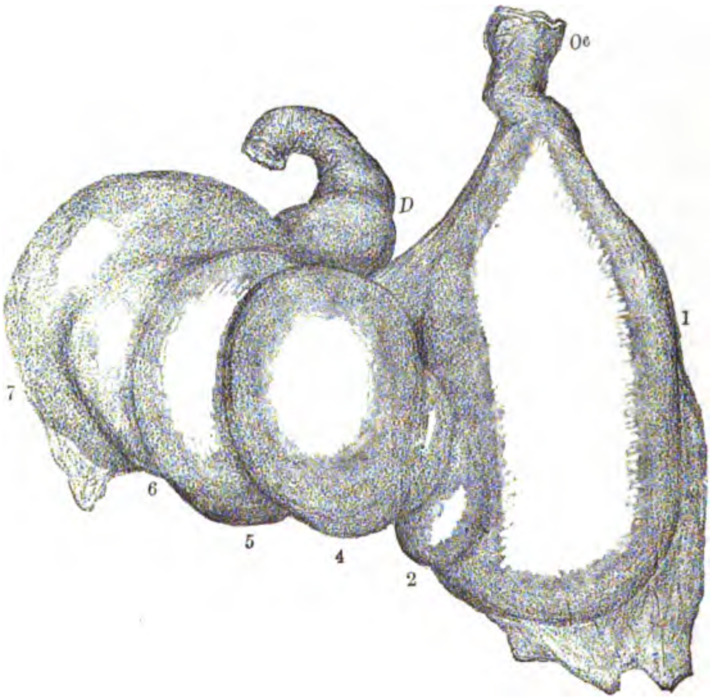


FIG. 2.—Stomach of *Hyperoodon rostratus*. *Oe*, œsophagus; *D*, duodenum. The numerals refer to the compartments of the stomach. The stomach was drawn so as to bring in the origin of the duodenum. The view-point, therefore, is somewhat forward, and the Λ-shaped form of the intermediate division is not distinctly shown in the figure.

valvular folds of mucous membrane which corresponded internally with the surface constrictions. These openings were not in the axis of the fold, but in proximity to the dorsal wall of the compartments.

The distal or pyloric division (7) consisted of a large compart-

ment, 12½ inches in its longest diameter and 9 inches in its widest, being about equal in size to both 5 and 6. It projected by a large rounded end to the right of the last compartment of the intermediate division, and from this end a broad omental fold, continuous with that from the intermediate division, hung pendulous. The opposite end of the pyloric division was wedged in between the dorsal surface of the 5th and 6th compartments and the commencement of the duodenum. This

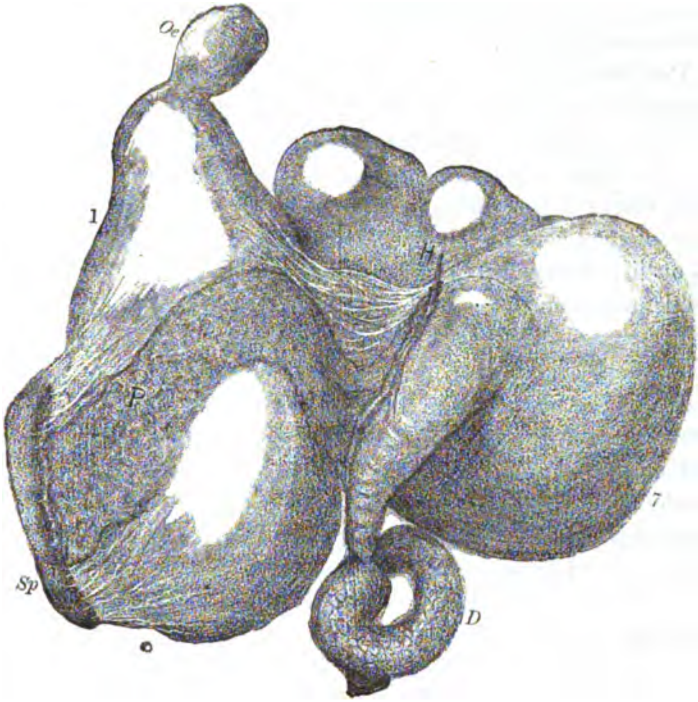


FIG. 3.—Dorsal surface of the stomach of *Hyperoodon rostratus*. *H*, hepatic duct; *Sp*, spleen; *P*, pancreas; *D*, cylindriform part of duodenum. The other lettering as in fig. 2.

division did not have any constriction on the surface to indicate either a partial or more complete separation internally into two or more chambers, but a well-defined constriction separated it on the one hand from 6, and on the other from the duodenum.

The Duodenum arose from the dorsal aspect of the pyloric division, so that its origin could not be seen from the ventral surface. It commenced as a funnel-shaped dilatation, which

was 12 inches long and 4½ inches in greatest breadth. It diminished in calibre as it passed away from the stomach, so that the narrow constricted end of the funnel was not more than 1 inch in diameter; here it became continuous with the cylindriform part of the duodenum, which widened out to a diameter of 2¾ inches. The mucous lining of the funnel was smooth on its surface, and valvulæ conniventes did not appear until close to its narrow end. The duodenum contained a quantity of the black horny beaks of the cuttle-fish on which the animal had fed.

The Hepatic Duct reached the dorsal wall of the funnel-shaped dilatation of the duodenum about an inch from the pylorus. It was almost as large as the human femoral artery, and was traced for nearly 4 inches in contact with the surface of the wall, where it was surrounded by lobules of the pancreas. It then pierced very obliquely the muscular and the mucous coats, its outline being visible without dissection, and opened into the duodenum about 5 inches from the narrow end of the funnel.

Pancreas.—This gland extended from the spleen to the commencement of the duodenum, where it surrounded the hepatic duct. It lay between the layers of the gastro-splenic omentum, across the dorsal aspect of the first compartment of the stomach, and on the dorsal surface of the funnel-shaped part of the duodenum. Its length was 15½ inches and its breadth was about 6 inches at the duodenal and 4 inches at the splenic extremity. In no part of its length had it any great thickness. It consisted of multitudes of dark brown lobules connected together by areolar tissue. The pancreatic duct was exposed on cutting into the substance of the gland, and was followed to its duodenal end to join the hepatic duct, where it was surrounded by lobules of the pancreas. The opening of the pancreatic into the hepatic duct was a little in front of the spot where the latter began to penetrate the duodenal wall, so that the terminal part of the duct and the orifice into the duodenum were common to both the pancreatic and biliary secretions.

Spleen.—The spleen was an elongated organ, 12½ inches in its antero-posterior diameter. It was widest about the middle, where it had a breadth of 2½ inches, and it was somewhat

attenuated at its two ends. Its connection with the proximal division of the stomach has already been stated.

This recent specimen of the stomach of Hyperoodon agrees with the dried specimen described in my paper of October 1885 in having seven compartments. In the dried specimen also they were arranged in proximal, intermediate, and distal divisions; the proximal and distal consisting each of a single compartment, the intermediate of five, two each in an anterior and a posterior limb, and one at the apex at the junction of the two limbs. It is now perfectly clear that the "elongated somewhat kidney-shaped sac," described in my previous paper, corresponds with the funnel-shaped dilatation of the recent specimen, and is therefore the commencement of the duodenum. John Hunter also described seven gastric compartments with a duodenal dilatation. Seven, therefore, is in all probability the usual number of compartments of the stomach of Hyperoodon, which possesses, therefore, only half the number of compartments present in Sowerby's whale. Occasionally, however, nine compartments are present, as in Eschricht's specimen, where, however, one of the nine was a sac-like dilatation of the œsophagus, and in a specimen recently described by Max Weber.

My recent dissections confirm the conclusions to which I arrived in my original paper on the stomach of the Ziphioid family of whales, that the first compartment does not correspond morphologically with the first compartment in the Delphinidæ, but with the second, and is a true digestive chamber, and that the first compartment in the Delphinidæ is absent in the Ziphiinæ.

Shortly after the publication of my former paper on the stomach of the Ziphiinæ, an admirable monograph on the Cetacea appeared by Professor Max Weber,[1] of Amsterdam, in which he gave an account of his dissection of the stomach of Hyperoodon.

Weber describes his specimen as consisting of an elongated cardiac compartment and of a pyloric part divided into eight semi-globular chambers, making nine in all. His pyloric part includes both my pyloric and intermediate divisions. In his

[1] *Studien über Säugethiere. Ein Beitrag zur Frage nach dem Ursprung der Cetaceen*, Jena, 1886.

specimen, therefore, the part corresponding to what I have termed the intermediate division consisted of 7 chambers, instead of 5 as in both my fresh and dried specimens, whilst the distal division, to which alone I have applied the name pyloric, formed the last compartment much larger than any of the chambers of the intermediate division. Weber has also recognised that the mucous membrane of the cardiac compartment is rich in glands, and differs essentially from the 1st gastric compartment in other Cetacea with its lining of œsophageal epithelium, and he came to a similar conclusion to that which I had arrived at in the previous year, that the 1st division of the stomach of Hyperoodon corresponds with the 2nd compartment of other Cetacea, and that the 1st or œsophageal compartment in them is wanting in Hyperoodon and perhaps in other Ziphioids.

It is very satisfactory to me to find my conclusions on this matter confirmed by the independent observations of so accomplished a naturalist as Professor Max Weber.[1]

DELPHINIDÆ.

Stomach of Phocœna communis.—Upwards of two centuries ago Edward Tyson gave an admirable account of the "Anatomy of a Porpess,"[2] and included in it a description, with a figure, of the stomach. Since then the anatomy of the organ in this animal has been described by various anatomists, including John Hunter, Sir Richard Owen, Robert Knox, J. B. S. Jackson, Arthur Jacob, and myself. It is unnecessary for me to say more in regard to the form of the stomach and the number of its compartments than that it consists, in succession from left to right, of a thin-walled, three-sided œsophageal compartment (1), lined by a squamous epithelium, with its base forward at the œsophagus, and its free apex directed backwards; of a

[1] Messrs John H. Scott and G. Jeffrey Parker have recently given a short description of the stomach of a Ziphius (sp. ?) caught in 1884 near Dunedin, New Zealand. The stomach consisted of ten compartments. The 1st or cardiac compartment was lined by a mucous membrane which they compare with the reticulum of the sheep's stomach. Eight compartments, mostly subglobular, made up what I have called the intermediate division, the first of which opened near the distal end of the cardiac compartment. The tenth compartment, next the duodenum, was elongated. The mucous lining of compartments (2–10) was soft and smooth.—*Trans. Zool. Soc. Lond.*, vol. xii. part 8, 1889.

[2] London, 1680.

cardiac compartment (2) not quite as large as the first, with numerous thick projecting folds of mucous membrane mostly running longitudinally; of a very small intermediate compartment (3) wedged in between 2 and 4; and of a long tubular pyloric compartment (4), which curves to the right, and becomes continuous with the subglobular dilated commencement of the duodenum.

This subglobular dilatation was lined by a smooth mucous membrane, but at the commencement of the cylindrical part of the canal the membrane was thrown into longitudinal folds. At the beginning of one of these folds was the mouth of the hepatico-pancreatic duct, through which a surgical probe could be passed along the duct as far as the transverse fissure of the liver. The hepatic duct was not dilated, and had no valve-like folding of its lining membrane.

As the microscopic characters of the mucous lining of the stomach are important factors in the comparison of the gastric compartments in the Ziphioid and Delphinoid whales, I have examined the mucous membrane of the three principal compartments of the stomach in the common Porpoise,[1] which may be taken as a type specimen of the Delphinidæ.

Vertical sections through the mucous lining of the 1st or œsophageal compartment, when examined under a low magnifying power, showed a thick layer of stratified epithelium, into the deeper part of which mucous papilla-like outgrowths of the corium projected. These were in all probability slender folds of the mucous membrane, which when vertically divided looked in section like papillæ. The sides and apices of these outgrowths were covered by numerous layers of epithelium.

Under higher powers the surface layers of epithelium were seen to consist of squamous cells, the nuclei in which were not very distinct. The deeper layers occupying the intervals between

[1] The examination was made on the mucous membrane of the stomach of an adult male. The œsophageal compartment was distended by a pultaceous mass of half-digested fish, the bones of which were in process of being "cleaned." Tyson states that Mr Ray found in the stomach of a Porpess "sand-eels, launces, or as called by Gesner *Ammodytæ*," also that Dan Major found the spines of fishes, small Tellinæ, particles of Testacea, Crustacea, and sand; whilst Tyson himself got in his specimen the spines of fishes and two or three nearly entire herrings. Tyson also saw the bones and spines of several fish in the œsophagus.

the outgrowths consisted of cells more polygonal in form, and the nuclei in which were very distinct. No glands were seen in the mucous lining of this compartment, which was obviously an extension of the mucous membrane of the œsophagus.

Vertical sections through the thick folds of mucous membrane of the 2nd or cardiac compartment showed it to be remarkably rich in elongated, tubular, branched glands containing peptic cells, so that, both in its general appearance to the naked eye and in its microscopic characters, it corresponded with the mucous lining of the cardiac compartment of the Ziphioid whales. The description which I gave in 1885 of the glands in the 1st gastric compartment of Sowerby's Whale (specimen A) applies almost verbatim to what I have seen in the 2nd compartment in the Porpoise. The glands are admirable examples of the "cardiac glands" of the stomach with their characteristic "peptic" cells.

Vertical sections through the mucous lining of the 4th or pyloric compartment showed it also to be highly glandular, but the glands differed in form and appearance from the cardiac glands. They were only about one-third their length, were less frequently branched, and the branching was apparently limited to the deep end. Their epithelial lining was so disintegrated that the shape of the cells could not be seen. The glands were of the type of "pyloric glands."

Stomach of Delphinus delphis.—Cuvier, in his *Leçons*,[1] describes the stomach of the Common Dolphin, which is in all probability this species. He speaks of five compartments, but his 5th compartment is apparently the same as what I shall describe as the subglobular commencement of the duodenum, whilst what he calls the long canal between his 2nd and 3rd compartments I shall name the 3rd compartment, so that his 3rd and 4th compartments are with me the 4th and 5th. Previous to Cuvier's description, Sir Everard Home had recorded[2] an account of the stomach of a small cetacean, which he names *Delphinus delphis* (Linnæus).[3] Dr J. B. S.

[1] *Leçons d'anatomie comparée*, t. iv., deuxieme partie, p. 79, 1835.

[2] *Phil. Trans.*, 1807.

[3] This animal was not *Delphinus delphis*, but probably either *D. tursio* or *D. albirostris*. From Home's figure and description, the stomach had only four chambers.

Jackson has also described and figured[1] the stomach of a fœtal Dolphin, the specific name of which he leaves in doubt, though in some respects he thinks it resembles *D. delphis.*

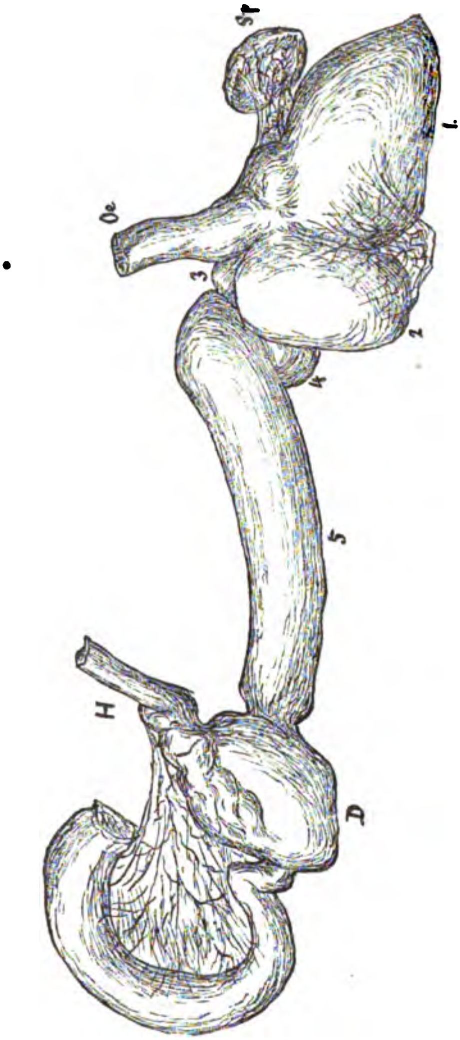


FIG. 4.—Ventral surface of stomach of *Delphinus delphis.* The lettering as in previous figures. The numerals refer to the compartments of the stomach.

The specimen which I examined was obtained from an animal shot in the Firth of Forth in 1887.[2] The stomach was removed

[1] *Boston Journal of Natural History,* vol. v. No. 2, October 1845.

[2] I have described the external characters of this animal in *Proc. Roy. Phys. Soc. Edin.,* vol. ix., 1887.

along with the surrounding viscera, the cavities were injected with spirit, and when the walls were hardened the compartments were opened into.

The Œsophagus, immediately after piercing the diaphragm, formed a pouch-like dilatation not unlike that described by Dr Jackson in his fœtal specimen. With this dilatation both the 1st and 2nd gastric compartments communicated. The mucous lining of the œsophagus was thrown into longitudinal ridges.

The Stomach consisted of five compartments. The 1st, or œsophageal, three-sided in form, with its base forward to the œsophagus and its free apex directed backward, was 5¼ inches long by 4 inches in greatest breadth. Its muscular wall was thin, and its mucous membrane was corrugated and formed narrow convolutions, covered by a thick layer of horny epithelium. The opening of this compartment into the œsophagus readily admitted two fingers.

The 2nd or cardiac compartment, subglobular in form, was to the right of the 1st compartment, from which it was separated by a deep cleft, but an omental fold passed from one to the other. It was 3½ inches long by 2¾ inches in greatest breadth. Its mucous membrane was raised into numerous thick projecting folds, the general direction of which was longitudinal, though these were connected together by short oblique or transverse folds. This compartment had two openings at its anterior end, the one into the dilated part of the œsophagus, which admitted the middle finger; the other was separated from the œsophageal opening by a fold of mucous membrane, it communicated with the 3rd compartment, and only admitted the tip of the little finger.

The 3rd compartment was situated in the angle between the œsophagus and the 2nd compartment; it was not as big as a walnut, and its mucous membrane was smooth.

The 4th compartment was behind and to the right of the 3rd, and was as big as a walnut. It communicated with the 3rd by an opening readily admitting a thick probe, and was lined by a smooth mucous membrane.

The 5th or pyloric compartment formed the tubular part of the stomach. It was 10 inches long, and passed from left to right, where it joined the subglobular dilated commencement

of the duodenum. Its left end was in contact with the walls of both the 3rd and 4th compartments. Its mucous lining was mostly smooth, though with some faint ridges. The opening into the 4th compartment admitted a large probe, whilst a similar sized opening communicated with the duodenum.

The subglobular dilatation of the Duodenum was the size of a small orange, and was situated at the right end of the tubular part of the stomach. The cylindrical part of the duodenum arose from it at the back of its right surface, and the opening between the two was large enough to admit the little finger. The mucous lining of this dilatation was smooth, except at the orifice of the cylindriform tube, where it was longitudinally folded. Half an inch from this orifice was the mouth of the hepatico-pancreatic duct opening obliquely at the end of one of these longitudinal folds.

The Hepatic duct was traced from the portal fissure, where it was formed by the junction of two large ducts emerging from the liver. The hepatic duct ran parallel to the portal vein, and was almost as large as that vessel. It was surrounded by lobules of the pancreas, and then reached the duodenal dilatation, to the wall of which it was attached. At first it was covered by the serous coat of the duodenum, and then pierced the wall to open on the mucous surface as above described. A probe could not be passed along that part of the duct which was in contact with the duodenal wall, for the duct was tortuous at this spot. As is well known, the gall-bladder is absent in the Cetacea, but this remarkably wide duct would obviously serve as a reservoir for the bile; the tortuous part of the duct, where it was in contact with the duodenal wall, would act like the spiral valve in the neck of the human gall-bladder.

The Pancreas was situated in relation to the dorsal aspect of the stomach, and extended as far as the duodenum and the hepatic duct. The pancreatic duct was exposed on dissecting into the substance of the head of the gland, and was followed to the part of the bile-duct surrounded by the lobules of the pancreas, which it joined about ¾ inch from the duodenum.

The Spleen was attached to the dorsum of the 1st gastric compartment by a broad gastro-splenic omentum. The spleen

was almost disc-shaped, and measured 2 inches in antero-posterior by 1¾ in transverse diameter.

Stomach of Delphinus (Lagenorhynchus) albirostris.—The stomach of the white-beaked Dolphin has been described and figured by more than one naturalist, and I may refer to the memoirs of Messrs J. W. Clark,[1] Cleland,[2] and Max Weber[3] for an account of it.

It is unnecessary, therefore, to go into much detail; but as I have been able to compare the stomach of an adult with that of a suckling calf,[4] there are some points to which I shall briefly refer.

The Œsophagus, after piercing the diaphragm, was dilated, and directly communicated both with the 1st and 2nd gastric compartments.

The Stomach was divided into four compartments. The 1st or œsophageal was 19 inches long and 12½ inches wide in the adult; 3½ inches long by 3¼ inches wide in the suckling calf. It had in both the usual form of this compartment in the Delphinidæ, with the base forward and the apex pointing backwards. The wall was relatively thin, and the corrugated mucous membrane was covered by a thick, yellowish, stratified, squamous epithelium. This compartment contained in the adult a large quantity of clean fish bones, probably whiting or haddock, together with otoliths and a few limbs of a crustacean like the common shore crab. Similar clean fish bones were also seen in the œsophagus and mouth.

The 2nd or cardiac compartment was 10½ inches long in the adult, and subglobular in shape. In the calf it measured about 3 inches both in length and breadth, and was separated from the 1st compartment by a deep cleft. Its mucous lining was elevated in strong folds, which to some extent were arranged longitudinally, but as short intermediate folds were numerous, and intersected each other, the arrangement was more reticulated than in the Porpoise. Max Weber, in his memoir, has given a figure of them, and states that the mucous membrane

[1] *Proc. Zool. Soc. Lond.*, June 20, 1876.

[2] *Jour. of Anat. and Phys.*, vol. xviii., 1884.

[3] *Tijdschrift den Ned. Dierkundige Vereeniging*, 1887.

[4] I have described the external characters of these animals in *Proc. Roy. Phys. Soc. Edin.*, December 19, 1888.

contains numerous tubular branched glands in which "peptic" cells are found. The 2nd compartment communicated with the 3rd by an opening situated in proximity to the œsophageal opening of the 2nd compartment.

The 3rd or intermediate compartment was in the adult as big as a small pear; in the calf about the size of a large hazel-nut. It was situated in relation to the dorsal surface of the 2nd compartment between it and the commencement of the 4th compartment, with which it communicated by a distinct opening.

The 4th or pyloric compartment formed the tubular stomach. In the adult it was about 12 inches long; in the calf only 4 inches. In both it curved to the right, and ended in the dilated commencement of the duodenum. The left end of this compartment projected into the angle of separation between the œsophagus and the 2nd compartment, where it formed a dilated cul-de-sac not unlike 4*a* in Max Weber's figure. The mucous lining both of the 3rd and 4th compartments was smooth.

The Duodenum was separated from the 4th compartment by a constriction, and the opening between them, large enough to admit a quill, was in the centre of a well-defined pyloric valve. It commenced by a large funnel-shaped dilatation, which was lined by a smooth mucous membrane. In the calf the hepatico-pancreatic duct opened on the surface of this mucous membrane, 2 inches from the pyloric orifice, on the summit of a ridge-like papilla. Immediately beyond the mouth of the duct the mucous membrane was elevated into valvulæ conniventes.

The Hepatic duct was attached to the wall of the dilated part of the duodenum for about 2 inches before it began to pierce its coats, and was enclosed by peritoneum. It was as large in the calf as the humeral artery, and in the adult as the common iliac artery of Man, and the lumen was much dilated. It was easily probed both from the hepatic and duodenal ends, but the probe could not be made to pass through that part which was in contact with the surface of the duodenal wall, apparently on account of the mucous lining being thrown into spiral folds. The hepatic duct was surrounded in the usual way by the pancreas, and the pancreatic duct opened into it close to the duodenum. Clark has figured the dilated hepatic

duct in his drawing of the stomach, and Cleland refers to its sacculated condition in his specimen.

The Spleen was attached to the dorsal surface of the 1st gastric compartment by an omentum. It was 2¼ inches long in the calf, much attenuated at its anterior end, and 1 inch in breadth near the posterior end.

Stomach of Monodon monoceros.—Very little apparently has been published on the stomach of the Narwhal. Dr Fleming, in his account[1] of a specimen, 12 feet long, stranded early in the century in Shetland, states that the stomach was divided into several compartments, and that the extent of its inner surface must be greatly increased by numerous cylindrical papillæ, some of them more than 2 inches long, which were dispersed over it. Meckel,[2] from the examination of a small fœtus, states that the 1st compartment was roundish, much smaller than the 2nd, and with the inner surface set with numerous strong, teeth-like projections arranged in compact longitudinal rows. He does not state the number of compartments, but I infer that he thinks there were three or five.

In September 1887, I received from Captain John Gray, of the whaling ship "Hope," a fœtal Narwhal, 5 feet 1 inch long, and therefore approaching the full term of utero-gestation. It had been preserved in salt, and was in good condition. I removed the stomach along with the surrounding viscera from the abdomen, injected the cavities with spirit, and, after it was hardened, opened into the several compartments.

The Œsophagus pierced the diaphragm, and 1½ inch beyond that muscle it opened into the 1st compartment of the stomach.

The Stomach consisted of five compartments. The 1st or œsophageal was 6½ inches long and 3½ inches in its greatest breadth. It was somewhat three-sided in outline, with its base forward at the œsophagus and the apex at the free posterior end. When opened into by a longitudinal incision, yellowish, horny cuticular-looking flakes of epithelium, often of considerable size, which had peeled off the surface, were lying loose in the cavity. When examined microscopically, they were seen to consist of stratified squamous epithelium. The surface exposed

[1] *Memoirs Wernerian Society*, vol. i., 1811.
[2] *System der Vergleich. Anatomie*, 527, vol. iv., 1829.

was smooth except for sparingly scattered papillary projections from $\frac{1}{8}$th to $\frac{1}{4}$th of an inch in length; but in proximity to the opening of communication with the œsophagus and to that into the 2nd compartment, the papillæ were crowded together in considerable numbers. These are probably the papillæ referred to both by Fleming and Meckel in their descriptions. The opening into the 2nd compartment was close to that into the œsophagus, a fold of mucous membrane covered with the papillæ alone separating them from each other. These openings were almost equal in diameter, and each readily admitted two fingers.

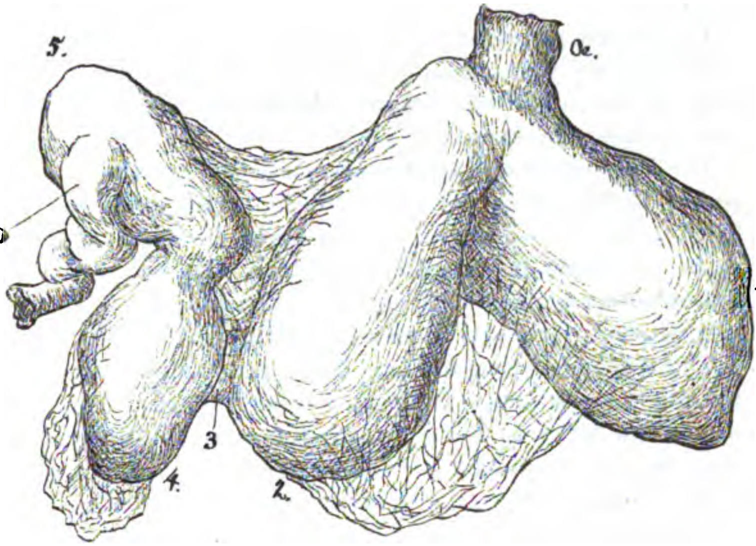


FIG. 5.—Stomach of a large fœtal *Monodon monoceros.* The letters and numerals are as in the preceding figures.

The 2nd or cardiac compartment passed backwards to the right of the 1st compartment, but was separated from it by a deep cleft. It was cylindriform in shape, 6½ inches long, and 2 inches broad. When opened into, the mucous lining was seen to form projecting folds, some of which were longitudinal, but others were shorter and intermediate in direction. The folds were not so strong or numerous as in Phocæna or Delphinus, and a portion of the mucous surface was comparatively free from them. They were crowded with branched tubular glands of the cardiac type in form and arrangement. The contained

cells were relatively large and granular, and obviously would become peptic cells in a stomach functionally active.

The 3rd compartment, about as big as a small walnut, was situated between the right side of the posterior end of the 2nd and the middle of the left side of the 4th compartment. It was scarcely visible on a surface view, and was only distinctly recognised after it had been opened into. It communicated with the 2nd compartment by an opening situated only 1½ inch from the free posterior end of the latter, and by the 4th compartment about midway between its opposite ends. The mucous lining was smooth.

The 4th compartment was situated immediately to the right of the 3rd, and passed from behind forwards. It was 3¼ inches long, 1½ inch wide, and generally cylindriform in shape. Its mucous lining was smooth.

The 5th or pyloric compartment proceeded from the anterior end of the 4th forwards and to the right, curving somewhat on itself, so that it had a convexity forwards. It was tubular in shape, and between 4 and 5 inches long. Its mucous lining was smooth, and it opened into the anterior end of the 4th compartment by an aperture which admitted a quill.

The Duodenum arose from the right and posterior aspect of the 5th compartment. It was somewhat dilated at its commencement, but soon became a cylindriform tube. Its opening into the 5th compartment readily admitted a quill. The mucous lining of the dilated portion was smooth, that of the cylindriform tube was elevated into valvulæ conniventes. Close to where the cylindriform part of the duodenum began was a semi-lunar fold of mucous membrane which bounded the orifice of the hepatico-pancreatic duct.

The Hepatic duct passed backwards and was not dilated as in *D. albirostris;* it became surrounded by lobules of the pancreas before it reached the wall of the duodenum. The Pancreas was in contact with the dorsal surface of the stomach from spleen to duodenum. The Spleen was attached to the dorsal aspect of the 1st gastric compartment by a broad gastro-splenic omentum. It was 2½ inches long and only ½ inch in breadth.

Stomach of Delphinapterus leucas.—Messrs Barclay and

Neill published in 1816[1] an account of the stomach of a White Whale (*Beluga*) killed in the Firth of Forth. They described four compartments, and pointed out the œsophageal character of the first. More recently descriptions of the stomach in this Cetacean have been given both by Professor Wyman and by Drs Watson and Young, and its division into five compartments has been recognised.

The specimen which I dissected was obtained from a young fœtus, only 13½ inches long, which was presented to me by Captain Phillips, of the whaling ship "Nova Zembla." From its small size I can do little more than record the dimensions and relative position of the five chambers of which it was composed.

The 1st compartment was of the usual form met with in the Delphinidæ. It was 1 inch long, and opened into the bottom of the œsophagus: its mucous membrane was corrugated.

The 2nd or cardiac compartment was closely attached to the right side of the 1st. It opened into the 1st compartment near to its œsophageal orifice. Its mucous lining was elevated into folds. Immediately to the right of the posterior end of the 2nd was the 3rd compartment, about the size of a large pea. The 4th compartment was placed ventrally, and to the right of the 3rd. It was about ¾ths of an inch long. The 5th or pyloric compartment commenced at the anterior end of the 4th, and extending for about 1 inch to the right, formed the tubular part of the stomach; it was bent on itself at its pyloric end, and joined the dilated commencement of the duodenum.

The stomach of this fœtus, that of the more advanced fœtal Monodon, and that of the calf White-beaked Dolphin all accord with what I stated some years ago in describing the stomach of Globiocephalus,[2] that in the fœtus and young stomach the paunch or œsophageal compartment is of about the same size as the 2nd compartment, whereas, when one of these Cetaceans acquires its nourishment independently of the mother, the paunch attains a great increase in relative magnitude.

From the foregoing description of the stomach in so many species of the Delphinidæ it is obvious that, whilst this organ

[1] *Memoirs Wernerian Soc.*, vol. iii., 1816.
[2] *Jour. Anat. and Phys.*, vol. iii. p. 118, 1869.

throughout the series is in many particulars constructed on a common plan, yet that there are differences amongst the different species. Each species possesses (*a*) an œsophageal or 1st compartment, lined by a prolongation of the squamous epithelium of the œsophagus, which has no representative in the Ziphiinæ; (*b*) a cardiac or 2nd compartment, with a richly folded mucous membrane closely packed with "cardiac glands"; it is a true digestive chamber, and corresponds with the 1st or cardiac division of the stomach in the Ziphiinæ; (*c*) a tubular, more or less elongated pyloric compartment continuous with the dilated commencement of the duodenum, and the mucous lining of which is packed with "pyloric glands"; it corresponds with the pyloric division of the stomach in the Ziphiinæ. The three compartments—œsophagéal, cardiac, and pyloric—are constant in the Delphinidæ, and form the chief chambers of the stomach.

But interposed between the cardiac and pyloric compartments is a variable number of small compartments, which are, I think, to be regarded as corresponding with the intermediate division of the stomach in the Ziphiinæ. In *Phocœna communis* and *Lagenorhynchus albirostris* only one such compartment is interposed, so that the maximum number of gastric chambers in these animals is four. In the Porpoise this intermediate compartment communicates with the second or cardiac compartment much nearer to its posterior than its anterior end; but in the White-beaked Dolphin the 3rd or intermediate compartment opens into the 2nd at its anterior end. In *Orcella brevirostris* Dr John Anderson describes[1] three compartments with "a narrow funnel-shaped channel between the 2nd and 3rd sacs," and this "channel" opens into the 2nd compartment in proximity to its communication with the 1st. I regard this "channel" as an intermediate compartment, so that the stomach of Orcella is of the same type of construction as that of the White-beaked Dolphin. The non-glandular structure of the œsophageal compartment, and the abundant glands in the mucous lining of the cardiac and pyloric chambers, are described by Dr Anderson.

In *Globiocephalas melas* (as I showed in my previous papers), *Delphinus delphis*, *Monodon monoceros*, *Delphinapterus leucas*,

[1] *Anatomical and Zoological Researches*, London, 1878.

Orca gladiator (Hunter), *Grampus rissoanus* (Murie), and *Grampus griseus* (Fischer), two compartments are interposed between the cardiac and pyloric chambers (though some writers speak of one of these compartments as if it were only a passage), so that there are five in all. These intermediate compartments are numbered in my description 3 and 4. Compartment 3 does not open into the 2nd or cardiac chamber at the same place in these various species. In *Globiocephalus melas* and *Delphinus delphis* it communicates with that chamber close to its anterior end, and a similar arrangement, according to Dr Murie, is found in *Grampus rissoanus*. In *Monodon monoceros* and *Delphinapterus leucas*, on the other hand, the opening is in proximity to the posterior end. The relation of compartment 4 to the pyloric chamber presents also some modifications. In Beluga and the Narwhal the pyloric chamber arises from the anterior end of compartment 4, and has no direct relation either to the wall of compartment 3 or to the anterior end of the cardiac compartment 2. In Globiocephalus and Delphinus, on the other hand, the left end of the pyloric chamber is in close relation to the walls of both these compartments. The Narwhal and Beluga, therefore, in their gastric arrangements, are more closely allied to each other than they are to the Common Dolphin and the Pilot Whale. The question also arises whether compartments 3 and 4, in such stomachs as those of Globiocephalus and Delphinus, strictly correspond with 3 and 4 in the Narwhal and Beluga. In the two latter it is evident that compartment 3 corresponds in position with compartment 3 in the Porpoise; whilst 3 in the Pilot Whale and Common Dolphin is in correspondence with 3 in the White-beaked Dolphin.

In the Delphinidæ there are also modifications in the relations of the œsophagus to the 1st and 2nd compartments of the stomach. In Phocæna, Monodon, and Beluga the œsophagus opens directly into the 1st compartment only, into the latter of which the cardiac chamber also directly opens. In *Delphinus delphis, Globiocephalus melas*, and *Delphinus albirostris*, both the 1st and 2nd compartments open directly into the bottom of the œsophagus. It seems possible, therefore, in these last named, for the food to pass directly into the cardiac chamber without entering into the œsophageal compartment.

In both forms, however, the anatomical arrangements would permit the regurgitation into the 1st or œsophageal compartment either of the gastric juice secreted by the glands of the cardiac mucous membrane, or of the constituents of the food after it has passed into the 2nd compartment, or of both. In *Delphinus albirostris*, for example, perfectly clean fish-bones have been found by several observers, including myself, in the œsophageal compartment. Now, as the mucous lining of this chamber is not glandular, the flesh can only have been removed from these bones by the action of the secretion of the cardiac glands, which probably had been poured into this chamber for the purpose; and the flesh soaked with and rendered pultaceous by the gastric juice had then entered the cardiac chamber in the furtherance of the digestive process, the bones being left behind. Or, as is, I think, less probable, the fish swallowed as food may have passed directly into the cardiac chamber, the flesh being there dissolved off the bones, and these latter, when clean, regurgitated into the œsophageal compartment. In either case the cleaned bones would be collected in that compartment, and then, by a further process of regurgitation, expelled by the œsophagus, pharynx, and mouth. The presence of clean fish-bones in the mouth of the adult White-beaked Dolphin which I dissected is evidence of the mode in which the animal gets rid of the undigested skeletons of the creatures on which it lives, a process which is more simple than if they had to travel along the several compartments of the stomach and the great length of intestine.

But the most remarkable instance of the mode in which those Cetacea which live on food containing indigestible or difficultly digestible substances, get rid of them, is furnished by the *Orca gladiator* dissected by Eschricht,[1] who found the skin of one of the many seals which it had swallowed partly hanging out of the mouth and partly contained in the mouth and throat. The animal had died whilst in the act of regurgitating the skin. In the œsophageal compartment of its stomach the remains of thirteen porpoises and thirteen seals were found, and the bodies of all

[1] "On the Northern Species of Orca," translated in the *Memoirs on Cetacea*, published by the Ray Society, 1866. In an Orca previously dissected by Professor Nilsson the stomach contained four seals with the skins on.

the seals were skinned, though slight traces of flayed skins were found in the stomach itself. Some of the animals appeared to be fresh flayed; most of them were half digested or already fallen to pieces, some only remaining in the shape of loose parts of the skeleton. A fourteenth seal, very small in size, much decomposed by digestion, had slipped into the 2nd compartment, though Eschricht thinks not until after death.

It is obvious that in this animal, as well as in the Porpoise which I dissected, referred to in the footnote on p. 477, the process of digestion was actively going on in the 1st or œsophageal compartment. This could only have been effected through the regurgitation of the secretion of the cardiac glands into that compartment. I agree, therefore, with the opinion expressed by Tyson, Sir Richard Owen,[1] and some other subsequent writers, that the 1st compartment in the Dolphins serves not only as a reservoir, but that the food undergoes a considerable change in it, due to the action of the gastric secretion regurgitated from the 2nd cavity. The food converted into a pultaceous mass can then pass readily into the 2nd and succeeding compartments, and the process of gastric digestion is completed by the action of the secretion of the glands of the pyloric chamber. It is obviously an advantage for the Dolphins, which swallow entire fish and other marine vertebrates, and where certain of the gastric compartments and apertures are small in size, to have a macerating chamber at the commencement of the stomach, in which the flesh can be separated from the skin and skeleton, and these indigestible materials at once placed in a position to be rejected at the mouth.

Hyperoodon, Sowerby's Whale, and the other Ziphiinæ do not have such a "macerating chamber" at the commencement of the stomach. With them the food, which is apparently largely composed of Cuttle-fish, passes at once into the cardiac compartment, to be subjected in it to the action of the gastric juice. The horny beaks, which are the only indigestible structures, are not regurgitated, but, as was shown by my specimen, pass through the several compartments of the stomach, and reach the intestine.

Both Cuvier and Meckel, in their systematic treatises on

[1] Note on p. 359 to John Hunter's article "On the Structure and Œconomy of Whales," *Collected Works*, vol. iv.

Comparative Anatomy, have remarked the variations in size of the Hepatic Duct. This was well shown in my dissections. In *Delphinus delphis* and *albirostris* the duct was so dilated as to serve as a reservoir for the bile, and the tortuous character of its canal before it pierced the duodenal wall would obstruct the rate of bile-flow into the duodenum. In Phocæna, Monodon, and Beluga the duct was not dilated. In Hyperoodon and Micropteron, although the duct was large, its lumen was not especially dilated.

(*Note.*—At the meeting of the Royal Society of Edinburgh, 18th March 1889, a paper was read, on the "Stomach of the Narwhal," by Dr Sims Woodhead and Mr Robert Gray, but the Proceedings of that date have not yet been published.)

LOOSE BODIES IN JOINTS. By G. M. HUMPHRY, M.D., F.R.S., *Professor of Surgery in the University of Cambridge.*

(From the *British Medical Journal*, September 19, 1888.)

I HAVE delayed replying to the able and courteous comments by Mr Sheild and Mr Howard Marsh (*Brit. Med. Jour.*, March 31 and April 14) on my letter ("Loose Bodies in the Knee-Joint," March 17) in order that I might give the consideration to the subject which their remarks demanded, and that I might examine certain specimens which I have only lately had the opportunity of seeing.

My statement was that we have a ready and sufficient explanation of the formation of these bodies in the growths from the synovial membrane into the joint; that only by an extraordinary and violent accident could a piece of cartilage or bone be broken off into a joint, and that necrosis could scarcely be credited as a cause.

With regard to the first of these points (the formation of loose bodies from the synovial membrane, which is generally admitted), I will go into a few particulars. The synovial membrane, which is continuous with the articular cartilage as its epithelium is continuous with that of the epithelium existing upon the surface of articular cartilage in early life, is prone, under morbid conditions, to the formation of cartilage and bone in its substance. This may take place in the villous processes which exist adjacent to the articular cartilages, about the lines of reflection of the membrane and at other parts, and which are not infrequently, in the normal state, found to contain cartilage cells; and it may also take place in the substance of the membrane, more especially in the vicinity of the articular cartilages, and sometimes as an outgrowth from them. A local irritation, a sprain, a wrench, or a blow may give rise to these villous outgrowths, or to one or other of them, in the otherwise quite healthy joint; and the villous outgrowths projecting into the joint becoming cartilaginous, and perhaps osseous, becoming also pedunculated, and finally detached, and losing, it may be, all trace of their former connection, constitute, as commonly admitted, the ordinary mode of formation of loose cartilages. This is more often observed to take place in a localised or isolated manner, so as to produce one or two loose cartilages, in early life, in young men and boys, whose active movements render them especially liable to sprains, and in the knee-joint, where the extent and reflections of the synovial membrane are so great and so numerous, where the range and variety of movements are exceptional, and where the leverage against the joint given by the long thigh and leg is greater than in the case of any other joint.

In some instances these bodies soon give rise to symptoms which lead to their removal. In others they remain before or after their detachment in snug quarters or recesses, and cause little trouble,

affording perhaps no indication of their presence, till by some particular movement, or strain, or blow, they are dislodged, get into inconvenient positions, give rise to the well-known symptoms, and are found slipping about in the cavity of the joint. Thus a man, aged 63, from whom I removed one of these bodies, stated that when he was a boy the "knee used to slip out of place at the inner side, and used to kink at the joint." Twenty years ago a piece seemed to break away; and from that time it used to slip about in the joint, and it became larger and more troublesome. A young gentleman had for years suffered weakness and uneasiness in the knee, and peculiar sensations at the back of the joint, consequent on a sprain in childhood; but the cartilage, which was quite loose, appeared in the front of the joint only a few weeks before I removed it.

A schoolboy, aged 15, whilst playing at football, fell with the left knee bent under him. He contrived to walk home, a distance of half a mile. Synovial inflammation followed, and was for some months easily re-excited, but subsequently subsided. Two years after, whilst walking in the street, he suddenly felt a severe stabbing pain in the joint, and was for some hours unable to extend it. Similar attacks, followed by synovitis, recurred, and a loose body was felt on the inner side of the patella. Having made a subcutaneous incision through the synovial membrane, I slipped the body into the tissue outside the joint, and secured it there. This was three years ago, and the body, which was about the size of a horse-bean, now feels about the size of a pea, and has given no trouble.

I removed a loose body from the knee of a young man, who experienced severe pain in the joint three months previously, when straddling across a ditch gathering watercresses. He was set fast and could not move from his position without assistance. The pain subsided in a few minutes, and he was able to walk and jump over a ditch. Next day the joint was swelled, and had to be kept on a splint. The loose body was discovered a few days afterwards. On two occasions, one three years and the other a year previously, he had experienced sudden pains in the knee, but less severe than the last attack.

During this period in which they remain in retirement, as it were, they may slowly enlarge,[1] and undergo calcification or ossification in the middle; and the section of such a body may show a nucleus or centre of true bone, with the characteristic corpuscles, imbedded in true cartilages, with the process of ossification from cartilage to bone progressing in the ordinary manner. These loose bodies are in some instances fibro-cartilaginous, in some cartilaginous, in some fibro-cartilaginous at one point and cartilaginous at another; and the cells near the surface may be, as seen in a specimen I have just examined (a loose cartilage of the ordinary type, with bone in the middle, recently removed from the knee of a young man), flattened out and lying parallel to the surface, whereas the deeper cells are more spherical

[1] One in the museum at Vienna, which still retains its connection with the capsule of the knee-joint, is said to be as large as the os calcis.—Tillmann's *Lehrbuch der Allgemeinen Chirurgie*, p. 467.

and arranged more or less in vertical columns, thus simulating very closely the structure of articular cartilage. Such a body may therefore present closely the appearance of a portion of bone and cartilage detached from the articular surface of a bone. I do not think the last feature has been previously pointed out; but in reality such arrangement of cells in the superficial and in the deeper strata is by no means, as seems to have been thought, peculiar to articular cartilage and to be regarded as diagnostic of it. It is indeed a feature common to cartilage in various parts and under various circumstances. Thus it is found in the costal and laryngeal cartilages, as well as in loose cartilages, also in the superficial layer of the cartilage covering ordinary exostoses in parts where the whole thickness of the cartilage is not occupied by the columnar arrangement of the cells preliminary to ossification.

My attention was first seriously drawn to the formation of these bodies from the examination of the loose body removed from the knee of the young man last mentioned, which consisted of bone and cartilage, was flat and oval (an inch by an inch and a half), and was on one side bare of cartilage, and presented a plain surface of bone, so that it much resembled a portion of articular cartilage and bone. Indeed, it was much like the specimen figured 4 and 5 by Mr Howard Marsh in the paper referred to. The explanation I then gave of the condition was, that during a long period of repose this body had not only undergone central ossification, but that one side of it, through contact with, and perhaps attrition upon, the femur or tibia, had been deprived of cartilage, and its bony nucleus had been laid bare. This view certainly seems to me much more probable than the supposition that it was the result of direct injury or of a process of necrosis separating it from any part of the articular surface of the bones. The view that in this and similar cases the origin and progress was such as I have mentioned derives corroboration from a specimen in the Pathological Museum at Cambridge, where a subspheroidal or flattened osseous body with cartilaginous margin hangs by a broad peduncle from the synovial membrane into the space between the patella and the femur. The cartilage from both the patella and the femur in the vicinity have disappeared, and the surface of each bone is somewhat worn away. It is quite certain that this pendulous body is a product of outgrowth of the synovial membrane from which it hangs, and not a detached piece of bone, and that the surfaces of the patella and the femur are in process of being worn away by its attrition; and it is almost as certain that it has, in like manner, suffered from attrition on both its surfaces, its cartilaginous covering having disappeared, and its osseous part having been exposed. So that we have here a good illustration of the effect upon one another of the pendulous body and the articular surfaces.

This view also derives corroboration from two specimens in the same museum—one being that of the knee with rheumatic arthritis, mentioned in my former letter, which I excised from a man, aged 60, in which there are many loose bodies of various sizes, some cartilaginous, some with osseous centres, some loose in the joint, some con-

nected by pedicles more or less broad with the synovial membrane. One of them occupies a concavity nearly large enough to hold it and adapted to it, in the side of the articular part of the tibia, and there can, I think, be little doubt that it, like the others in the same joint, had its origin in the synovial membrane, and that it had gradually, by pressure and friction, led to the formation of the cavity in the tibia in which it lies. In the other specimen, a loose, tuberated, bony nodule, with cartilaginous covering, larger than a filbert, is lodged, for about one-third of its thickness, in a fossa in the outer and fore part of the internal and articular surface of the tibia, which has evidently been formed by the pressure and friction of the body; and the tubercles on the side of the body opposed to it have been rubbed down so as to present a nearly smooth osseous surface. The cartilage has in great measure disappeared from the corresponding femoral condyle; and it is remarkable that movement of the joint can have taken place, notwithstanding the presence of such a body in such a position. There are villosities of the synovial membrane and "lipping" of the articular margins.

Specimen 1926, in the College of Surgeons, furnishes still better evidence of the process. In it a foreign body, an inch in its greatest diameter, attached to the crucial ligaments, has, by friction and constant pressure, worn for itself a deep cavity, with grooved walls, in the posterior and lower part of the outer condyle of the femur in which it lay imbedded and apparently immovable, and a second smaller body having similar attachment appears to have begun to wear a hole on the inner side of the under part of the internal condyle. In the museum of the Middlesex Hospital (No. 710) is a pointed fibrous growth, 1½ inch long, hanging by a narrow neck from the posterior attachment of the internal semilunar cartilage, and lying upon the articular surface of the tibia. Whether it has begun to make an impression upon that surface cannot be seen, but that it would soon have done so if it had continued in that position and gone on enlarging and hardening there can be little doubt. In a recent specimen in the same museum is a loose body, like a miniature patella, lying in a bare cup-like depression of the femur above the outer condyle; and in St George's Museum, III., 44 b, is a smaller pendulous body hanging in a cavity above the coronoid fossa of the humerus.[1]

It is clear that in these cases the bodies were of long standing, had slowly grown and hardened, and had gradually—very gradually—worn, or were in process of wearing, for themselves nests in the bones on which they laid, and they might at any time have become quite detached and lost all trace of their former synovial attachments. During the time of their repose they would have caused little or no inconvenience. It would have required a considerable force, such as a violent strain or blow, to dislodge them, to bring them into notice, and to cause them to give rise to the symptoms which indicate the presence of a loose body. Their existence would thus, not improbably,

[1] It is represented in the *System of Surgery*, by Holmes and Hulke, ii. 355; and in the College of Surgeons (1927) are two "pendulous masses of bone and cartilage" in the olecranon fossa.

be dated from the time of their dislodgment, and their origin would be attributed to the force which had dislodged them. Thus the "irregular nodule of bone" (Museum of College of Surgeons, 1931), one side of which is bare and the other covered with substance which looks like cartilage, and which presents "no indications of its ever having formed a part of articular surface, and no broken part to show that it separated from any pedicle," was removed by Mr Barwell from a retired army surgeon, aged 43, subject to rheumatic arthritis. Two months before it was removed he struck his knee sharply, and the next day he found a loose body in the joint. He had no synovitis or pain. He then missed a bony lump which he had noticed previously over the inner condyle. So also the large loose body (in the same museum, 1935), nodulated on one side, flat on the other, partly bony and partly cartilaginous, which presented "no evidence that it ever formed part of the normal surface of a joint or was ever pedunculated," and which was excised from a man, aged 40, and presented by Sir William Fergusson, was detected after a severe twist of the knee. A young man in Addenbrooke's Hospital sprained his right knee while boxing, was carried home, and kept his bed for a fortnight. He then perceived a loose substance in the outer part of the joint. After a month he could get about pretty well. As he experienced inconvenience from the substance, he came into the hospital and it was removed. I am informed that it showed no sign of having been detached from an articular surface, and presented the ordinary appearance of a loose cartilage, being about the size and shape of a strychnine nut. The joint was, to all appearance, quite sound before the injury. Instances of the discovery of these bodies soon after injury are also given in Hey's *Surgery;* in one case there were two in the same knee, the fact of there being two precluding the idea of their being the direct result of injury.

It is well known that in rheumatic arthritis these cartilaginous and osseous bodies are very liable to form in the synovial villi, which commonly enlarge in this disease; and these may be found to have become detached in great numbers. They also form in the synovial membrane, and possibly in the subsynovial tissue, and often in close proximity to the articular cartilage.

When thus situated they may grow into contact with, or encroach upon, the thickened, outgrowing, nodulated, and "lipping" margins of the articular cartilage so often met with in rheumatic arthritis. In this borderland between cartilage and synovial membrane it is not always quite easy to tell in which of these structures the osseous bodies were formed; and of two observers, one will judge that they have originated in continuity with the articular cartilage and are in process of separation from it, while the other will conclude that they have originated in the synovial membrane, and are in process of encroaching upon or coalescing with the abnormally projecting articular cartilage. The latter, which I believe to be the more common, may be often proved by noting the manner in which the several stages of growth in the membrane with approximation to the cartilage are evidenced at different parts in the same specimen. The edges of the

projecting and overhanging lips of articular cartilage do, however, sometimes grow out irregularly with intervening spaces. This is well seen in specimen 709 in the museum of Middlesex Hospital; and it is possible that they may become detached from their bases, though I have not seen an instance in which it seemed very probable that this had taken place.

It is, therefore, sufficiently proved that a loose body formed in the synovial membrane may (1) come very closely to resemble, microscopically and to the naked eye, a portion of articular cartilage and bone; may (2) in course of time form, by its pressure and friction, a fossa in the articular end of a bone more or less adapted to it, in which it may lie without giving rise to any particular symptoms, from which (3) it may become dislodged and first excite attention in consequence of a blow or strain, and so lead to the presumption, which may seem to be confirmed by microscopical examination of the loose body and even by examination of the joint, that it had been detached from the articular end of the bone by the blow or strain from which the symptoms of its existence were dated. It appears, moreover, that this is no very infrequent sequence of events, and that it may occur in a joint which presents no other indication of disease.

I should add that the presence of a loose, or nearly loose, body in the knee, caused by the tearing off one end of a semilunar cartilage from its attachment, and its nearly complete severance from the rest of the disc, has been instanced by Mr Broadhurst (*St George's Hospital Reports*, vol. iii.), and by the specimen shown by Mr Bowlby at the Pathological Society on April 17.[1] Possibly also loose bodies may occasionally originate in fibrinous masses effused into the joint after the manner often taking place in ganglions.

The dominance in my mind of the view I have expressed, as to the manner of formation of loose bodies in joints from the synovial mem brane, may have led me to write in rather too strong terms against the view that they may also be formed by the detachment of portions of articular cartilage and bone by accident or by necrosis, and though on the former point I give in a little, on the latter I am still *tenax propositi.*

With regard to the former of these modes of detachment—namely, by accident—I am not aware that any reliable instance has yet been adduced of the formation of a loose body by the breaking off of a piece of articular cartilage or bone by a blow; and we can scarcely conceive such an occurrence without greater damage to the joint than appears to have taken place in any recorded case of loose body in the synovial cavity.

The specimen which has been referred to by Mr Howard Marsh, in

[1] Since the above was written Mr G. B. Gifford has sent me a portion of the external semilunar fibro-cartilage, which he removed fnom the knee of a man aged 27. It was attached only to the head of the tibia near the spine. Two years previously the man fell roughly on his left knee; in six weeks was able to walk. Ten days before the operation, when rubbing his feet on a mat, he felt something spring out in the knee. This something went out and in on moving the knee, causing much pain and inability to walk. The specimen is in the University Museum.

St Thomas's Museum, of a fragment of cartilage and bone, taken by Sir John Simon from the knee-joint of a man, and judged by him to have been detached from the articular surface by a wrench in falling three weeks before its removal, cannot perhaps now, in its bottle, be sufficiently determined. Its minute examination, however, by Mr Shattock is, I believe, confirmatory of the view of Sir John Simon. The accident to which it is attributed was followed only by some inconsiderable synovitis. Mr Teale has been so good as to send me for inspection the fragment represented by him in a woodcut in the *Brit. Med. Jour.*, May 26, p. 1109; and its rough (fractured) bony surface on one side, and articular cartilage on the other, as seen in the bottle, leave no doubt, I think, that it was, as he concludes, broken off from the articular surface of the patella by the severe wrench which he describes. Possibly it was broken off by a violent wrench against the margin of the femoral condyle, and the St Thomas's specimen may have been due to the same cause. At any rate, it must be admitted that these are two instances of the production of loose bodies in the joints by accident.

Weichselbaum[1] goes into this question, and gives the account of the elbow-joints of a strong male subject, aged 20, in each of which was a loose body, occupying a vacancy in the part of the articulating margin of the head of the radius which plays in the lesser sigmoid cavity of the ulna. The form and adaptation of these to the vacancies in the two radii, and the absence of other disease, leads him to the conclusion that they were the result of fracture. In what manner symmetrical fractures in those particular situations could occur, he does not suggest, and it is not easy to conjecture. It is further to be observed that each of these bodies was more than large enough to fill the vacancy in the head of the radius, and was composed of hyaline cartilage, fibro-cartilage, calcified cartilage, and bone, and that the thickness of the cartilage exceeds that of the head of the radius. These points he endeavours, but insufficiently, to make tally with the supposition that the bodies had been broken off from the bones, in the hollows of which they were placed. It is quite as probable that these were congenital as that they were separated by fracture. Is it not more probable that they were the result of disease? In two nearly symmetrically rheumatoid elbows in the College of Surgeons (1928–9), besides other bodies which were nearly loose, but attached—one in front and one behind the joint—there appears to be a body to the retiring angle in front of the radio-ulnar joint on each side. The coronoid process also looks as if it had been truncated by the presence of one of the bodies which, if it had been solitary, might have been supposed to have been broken off from it.

The occurrence of loose cartilages in the corresponding joints of the two sides has been observed in several cases, and I need scarcely say that such symmetrical occurrence is scarcely compatible with their being the result of injury.

Mr G. A. Syme[2] removed a loose body from the right elbow-joint

[1] "Zur Genesis der Gelenkkorpen," Virchow's *Archiv*, lvii. p. 127.
[2] *Australian Medical Journal*, July 15, 1888.

of a man aged 22. Five years previously there was a slight wrench of the joint, followed by pain and swelling, which subsided, and he felt no further inconvenience for three years, when, "while holding up the shafts of a heavy dray, it overbalanced, and he was thrown violently to the ground on his back. He retained his hold of the shaft with his right hand, and, keeping it supported off the ground, felt a strong 'jar' in the right elbow which rested on the ground. The joint became very painful, and he found he could neither straighten nor fully bend the arm; and, when he did attempt to straighten the arm, a 'lump' appeared on the outer side of the joint, but disappeared on his touching it." Efforts to keep the lump in place failed; the use of the arm was in great measure lost. Mr Syme accordingly removed it. He says:—"From the history given of the previous inflammation in the joint and the nature of the accident, I thought that the body was probably an hypertrophied fringe of synovial membrane that had become pendulous and then been detached by the accident;" and the account he gives of the specimen certainly does not seem to justify his departure from that very probable view, for, although "it consists of true bone covered on its (presumably) upper and outer surfaces by articular cartilage," which appearance, I have shown, is not uncommon in loose cartilages formed in the ordinary way, yet "on the other surface (presumably the line of fracture) it is covered by fibrous tissue"—a condition much more indicative of loose cartilage than of a fragment of articular surface detached by accident. The size and shape of the body are not given, nor the extent to which the cartilage surrounds the bone, which, be it remarked, is stated to have "an areolar appearance, as if recently ossified."

With regard to necrosis as a cause of loose bodies such as I am discussing, I must confess that the process of exfoliation, or "quiet necrosis," as it has been designated by Sir James Paget, was not in my mind when I wrote (17th March), and is not mentioned in the work to which I have referred. This, no doubt, sometimes occurs in bones, a portion dying and being slowly detached beneath the periosteum with little or no suppuration. A good instance is furnished by the bone of a calf in the Cambridge Museum, on the shaft of which is a broad, raised, sharply-defined table bone; and, on making a section, I found a loose sequestral scale, half an inch in diameter, lying in a completely-closed cavity; but it requires rather more evidence than we yet have that, in an otherwise healthy joint, a portion of bone and cartilage, presenting to the naked eye and under the microscope quite a natural appearance, has been the seat of necrosis, and has in consequence been separated. Surely the death—the necrosis, however quiet—of a portion of articular cartilage and bone must leave some structural traces of the process by which that death was brought about, and which attended upon it; and a necrotic piece of bone and cartilage could scarcely present the perfectly normal character which the loose bodies supposed to have been thus detached are said to have had.

Still I could not help feeling that the very remarkable and interest-

ing case given by the late Mr Teale in vol. xxxix. of the *Medico-Chirurgical Transactions*, and quoted at length by Mr Howard Marsh, did seem to justify this view. My good friend Mr Teale has, however, kindly sent me the specimen from the Leeds Museum for examination. I find that the loose body does, as described, present very much the appearance of a portion of articular cartilage and bone, and is nearly adapted to the space in the condyle of the femur from which it is supposed to have been detached by some necrotic process. On the other hand, it was situated on the under and outer part of the internal condyle, a very sheltered spot, where a blow even from a beer barrel could scarcely cause the change in question. Secondly, the cavity in which the loose body lay is at one part continuous with the intercondyloid fossa, a situation in which synovial growths have a tendency to form and to work their way into the surfaces of the condyles, especially that of the internal condyle. Thirdly, the articular margins present—in no very marked degree, it is true—the lipping indicative of rheumatic arthritis, in which disease, we know, synovial growths are very liable to form. Fourthly, the cavity in the condyle occupied by the loose body is smooth, slightly uneven, with a well-defined edge of cartilage, and presents no indication whatever of ulcerative or other process by which the loose body can have been detached, but rather that of absorption from pressure. Fifthly, at the circumference of the loose body the cartilage is projected into a flail-like edge, and above this edge it extends, with a smooth contour, upon the upper or applied surface of the body, where it gradually fades and is partially continuous with the cartilaginous nodules next to be mentioned. Lastly, the upper or deeper surface of the loose body—that applied against the condyle—is slightly knotty or tuberculated; and these tubercles are found, on microscopical examination, to be composed of true cartilage, which is continuous with the cartilage of which the body is composed. In this cartilage calcification has taken place at parts, but no trace of bone is to be found. These features, especially those last mentioned,[1] seem to preclude the possibility of this body having been detached from the articular surface by necrotic process or in any other way, in spite of the peculiar circumstances which favour the view taken by Mr Teale and others, and to accord, on the whole, best with the supposition that the body was an outgrowth from the synovial membrane, which gradually formed for itself the cavity so nicely adapted to it. The same remark must, I think, apply to the layer of fibrous tissue found in the corresponding situation on each of the symmetrical bodies removed from the otherwise healthy knee-joints of a young man by Mr Holden, quoted by Mr Howard Marsh.[2] It can scarcely be supposed that this tissue would have been formed upon a surface separated by necrosis

[1] The flail-like edge of this body and the tuberculated character of its applied surface, with the border of cartilage remaining upon that surface, are fairly represented in the figure at p. 788 of this *Journal* for April 14th.

[2] *St Bartholomew's Hospital Reports*, vol. iv. p. 256; and *Brit. Med. Jour.*, April 14.

from the articular end of a bone. This remarkable case is to some extent paralleled and probably elucidated by that reported in the *American Journal of Medical Science*, October 1848, in which two oval flat bodies weighing, one 283 grains, and the other 257 grains, and measuring $2\frac{1}{15}$ inches by $1\frac{1}{16}$ and $\frac{5}{8}$ in thickness, and the other $2\frac{3}{8}$ inches by $1\frac{1}{16}$ and $1\frac{2}{16}$ in thickness, were removed from the knees of a man aged 43, who recovered from the operations and was able to walk with perfect ease. That these bodies were of synovial origin is rendered probable from the statement that he had swelling and severe pain in the knees when he was 17; and three years afterwards he found a movable body just above the right patella, and, after a short interval, a similar body in the left knee. A cast of these bodies in the College of Surgeons' Museum shows them to have been uneven on the surface.

In the case carefully described and figured by Klein,[1] where two bodies, each composed of a layer of cartilage and a layer of bone, occupied a fossa in the outer part of the internal condyle of the femur, the idea of their having been separated from the articular surface is negatived—first, by there being two bodies; secondly, by one of the bodies still retaining its connection with the synovial membrane, thus indicating its origin; and, thirdly, by the cartilaginous coverings extending over the smooth edges of the loose bodies, upon their applied surface beyond the deeper level of the surrounding articular cartilage. This last point—the extension of the cartilaginous covering in a smooth manner over the edge of the loose body on to its applied surface, between that surface and the bony surface of the cavity of the condyle—may, I think, be taken as a proof, in any case, that the loose body has not been separated from the articular surface either by necrosis or direct force, but that it has been formed independently, and that, by friction and pressure upon the condyle, it has rubbed a cavity in it, and has been more or less completely deprived of its cartilaginous covering on one side. If this test be applied, it will, I think, be found to indicate the improbability of detachment by necrosis in most, if not all, of the instances with regard to which that view has been entertained. It does so in the cases just mentioned, as well as in the second case represented by Mr Teale in the *Brit. Med. Jour.*, May 26, p. 1109 (which specimen I have had the opportunity of seeing), where there were two loose bodies, one of which retains attachment to synovial membrane; and another loose body in the same specimen shows well the usual effects of rubbing on one side. It does so in the instance represented by Cruveilhier,[2] and often quoted as an example of a loose body detached from the articular surface. It does so, as far as I can judge, in the case of the loose body (No. 947 or 647) in the College of Surgeons referred to by Mr Howard Marsh, which also looks as if there were some remnants of cartilage upon its bony, or applied, surface. In the

[1] Virchow's *Archiv*, xxix. 190.

[2] *Anatomie Pathologique*, livraison ix. pl. 6, fig. 3, and copied by Bardeleben, *Chirurgie*, ii. 637, fig. 87.

specimen in St George's Museum (III. 140), which has been elsewhere referred to, the loose body is not apparent; but the cavity which it occupied in the condyle is in the situation into which, as I have before said, bodies formed into the adjacent part of the synovial membrane are liable to intrude themselves.

Mr Bernard Pitts showed me a specimen in St Thomas's Museum, in which from the under part of a condyle of the femur, in each of two knee-joints of the same person, a flake of cartilage, about a quarter of an inch in diameter, appears to be in process of separation, and its flocculent deeper surface is still connected by threads to the fossa in the cartilage from which it is being detached. The patient was under 30, but the effects of rheumatic arthritis are shown in the extension of the articular margin, and in a slight villosity of the synovial membrane, also in fibrous or velvety degeneration of the articular cartilages, especially in the neighbourhood of one of the separating fragments; and it seems probable that the separation of these fragments was being brought about by a modification of that change in the cartilages which is so common in rheumatoid disease. This view derives confirmation from the presence of cartilaginous bodies, such as I have mentioned, in the synovial membrane. In what number these existed, and whether any of them were pendulous in the joint, is not now apparent.

The conclusions, then, at which I arrive are:—

1st. Although I am not aware of any instance in which a portion of articular has been detached by a blow, yet in two cases (Simon's and Teale's) this appears to have resulted from a violent wrench. In each case the loose body so formed was removed by operation.

2nd. In none of the instances that I have read of, in which the formation of a loose body has been attributed to necrosis, does the evidence of such process appear to me to be satisfactory. The resemblance in structure of certain of these bodies to articular bone and cartilage as an argument in favour of that view, and it was perhaps the strongest, is, in a great measure, set aside by the discovery that this resemblance exists, also, in loose bodies formed in the ordinary way, namely, by synovial outgrowth; these being found in microscopical characters and general features much to resemble portions of articular bone and cartilage. They may, however, be distinguished by one or more of the following features:—(1) The presence in greater or less amount of fibro-cartilaginous or fibroid, as well as cartilaginous tissue in the body. (2) The imperfect denudation of the bone upon the rubbed down, or applied, surface of the body, so that remnants of cartilaginous or fibro-cartilaginous or fibroid tissue are found there. (3) The varying thickness of the cartilaginous covering, which in some parts may exceed that of normal articular cartilage, and its extension over the rounded edge of the body, to a greater or less extent, upon the circumference of its applied surface. (4) The knotty outline of the osseous nucleus and the imperfection of its bone-formation. (5) The size of the loose body being greater than that of the cavity in the condyles, so that it rises above the level of the surrounding articular

cartilage. The presence of any one of these features renders a derivation from the articular surface very improbable; and the combination of two or more of them renders it almost impossible.

Recently, in a knee in this dissecting-room, two quite loose cartilages with ossifying nuclei were found—one, of the size of a pea, under the fore part of the external interarticular cartilage; the other of the size of a bean, upon the middle of the same interarticular cartilage, which was here softened and partially destroyed. The latter, by its pressure upon the femur, had caused softening of the articular cartilage in a limited area; and the softened portion, together with a thin layer of subjacent bone, was in process of separation. The specimen is in the University Museum, and is interesting as showing a necrotic state of cartilage, with the changes observable in cartilage under this condition.

AN UNUSUAL ARRANGEMENT OF THE PSOAS MUSCLE.

By R. D. Clarkson, B.Sc., and Harry Rainy, M.A., *Students of Anatomy, University of Edinburgh.*

In the early part of the present winter session we observed, in the course of dissection of a middle-aged male subject, an unusual subdivision of the psoas muscle, there being apparently four psoæ on each side. On the *right* side the *psoas magnus* arose by mixed fleshy and tendinous slips from the sides of the bodies and anterior surfaces of the transverse processes of the upper four lumbar vertebræ, from the tendinous arches over the lumbar arteries, and from the sides of all the intervertebral discs between the last dorsal and the 5th lumbar vertebra. It also took origin from a slender tendinous arch which passed outwards from the fascia at the level of the 1st lumbar intervertebral disc to about the middle of the last rib.

The *psoas parvus* took origin by fleshy fibres from the side of the body of the 1st lumbar vertebra and upper part of the side of the body of the 2nd lumbar vertebra, and from the fibrous arch crossing the first lumbar artery. Its course was downwards, in front of the psoas magnus, to terminate in a long tendon, which, about 3 inches above Poupart's ligament, spread out into the iliac fascia, through which it was inserted into the ilio-pectineal line. From the under surface of the tendon, at the point where it formed the above expansion, a few muscular fibres arose and formed a narrow sheet of muscle, which passed downwards to fuse with the internal surfaces of the iliacus and psoas muscles.

The *psoas tertius* arose from the inner half of the 12th rib, in intimate connection with the insertion of the quadratus lumborum, and also from the tips of the transverse processes of the first four lumbar vertebræ between the origin of the psoas magnus and the insertion of the quadratus lumborum. It passed downwards, in front

of the quadratus lumborum and iliacus, and ended in tendinous fibres, which fused, near the level of Poupart's ligament, with the tendons of the psoas magnus and psoas quartus.

The *psoas quartus* was a small muscle which arose, by a small fleshy slip, from the anterior surface of the lower and inner part of the tendon of the quadratus lumborum; also by a larger slip from the transverse process of the 5th lumbar vertebra, and from the intertransverse ligament in its inner half. It passed downwards, to fuse with the tendons of the psoas magnus and psoas tertius, at the level of Poupart's ligament.

All the above muscles were separated by distinct cellular intervals, in which ran branches of the lumbar and ilio-lumbar arteries for their supply. Branches of the anterior crural nerve were traced into each division of the psoas.

On the *left* side the *psoas magnus* and *psoas parvus* had their origins, course, and insertions, similar to those on the right side; but there were no fibres arising from the tendon of the psoas parvus to correspond with those described on the right side. The *psoas tertius* took origin from the anterior surfaces of the transverse processes of the 3rd and 4th lumbar vertebræ, and had an insertion similar to that on the right side. The *psoas quartus* arose by two slips from the transverse processes of the 4th and 5th lumbar vertebræ. The course and the insertion were as on the right side.

The above arrangement appears to us the more noteworthy, in that it exhibits several interesting points of resemblance to the disposition of the psoas in the Seals, which we will now proceed to indicate.

The descriptions of the muscles in the various Seals are taken from Dr Strettell Miller's account of the myology of the *Pinnipedia* in the "Challenger" *Report on the Seals* (Zoology, vol. xxvi. part lxviii. pp. 176–179).

In *Arctocephalus gazella* the psoas magnus "arises by a series of muscular slips, from the posterior halves of the last four dorsal vertebræ, from their intervertebral discs, *and from the ventral surfaces of the ribs* and the ligaments of the rib joints. In the lumbar region it arises from the whole of the ventral surfaces of the 1st, 2nd, 3rd, and 4th lumbar vertebræ, and from their intervertebral discs and transverse processes." The origin here described from the ribs resembles the unusual origin from fascia reaching outwards to the last rib, which we have described for the psoas magnus.

In *Macrorhinus leoninus* the psoas magnus "is inserted into the posterior ventral spine of the ilium, *which is fused with the pectineal eminence.*"

May not, therefore, the psoas parvus of human anatomy be a part of the psoas magnus retaining this attachment? The muscular slip described as arising from the under surface of the tendon of the psoas minor on the right side would support this view.

In other respects the greater part of the psoas magnus in Man and the Seals is doubtless homologous.

The psoas parvus in a large *Phoca vitulina* arose "from the ventral

surfaces of the 14th and 15th ribs and their rib-joints, from the sides of the 14th and 15th vertebræ (dorsal?), from the ventral surfaces of the bodies of these vertebræ, and from the ventral surfaces of the transverse processes of all the lumbar vertebræ." In a smaller *Phoca vitulina*, *Phoca barbata*, *Phoca hispida*, *Macrorhinus*, and *Arctocephalus* it arises from the tips of the transverse processes of the 2nd, 3rd, and 4th lumbar vertebræ.

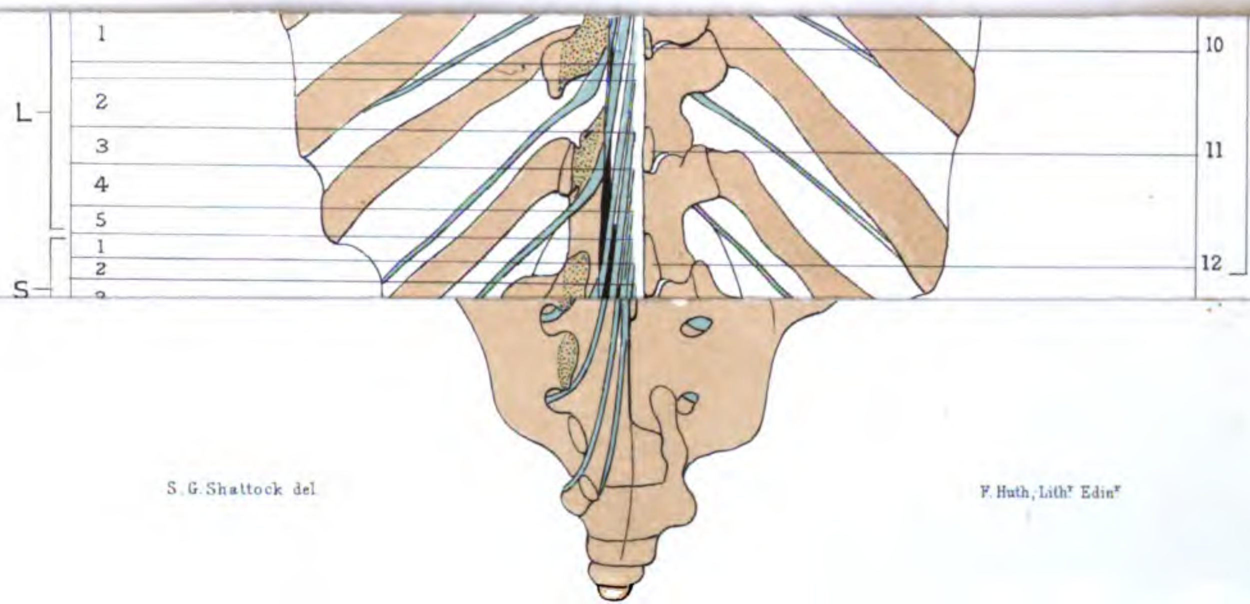
Its origin is thus, in all cases, associated with transverse processes of lumbar vertebræ, and, when more extensive, with the ventral surfaces of ribs and dorsal vertebræ. Therefore, it is equivalent to the psoas tertius hominis.

The psoas tertius in Seals is almost exactly homologous with the psoas quartus hominis. Thus, in *Arctocephalus gazella* the psoas tertius arises "from the sides and ventral surfaces of the lower border of the second last lumbar vertebra, from the upper half of the same part of the last lumbar, and from the intervertebral disc between it and the 2nd lumbar, and from the root of the transverse process of the last lumbar."

The homologies thus indicated may be represented in the accompanying table :—

Seals.	Man.
Psoas magnus, ...	{ Psoas magnus. { Psoas parvus.
Psoas parvus, ...	Psoas tertius.
Psoas tertius, ...	Psoas quartus.

Vol. XXIII / N.S. Vol. III} Pl. XIII.



S. G. Shattock del.

F. Huth, Lith.r Edin.r

Drawing of a dissection made by R. W. Reid, showing the relation between the superficial origins of the post.r roots of the spinal nerves and the spinous processes of the vertebrae.

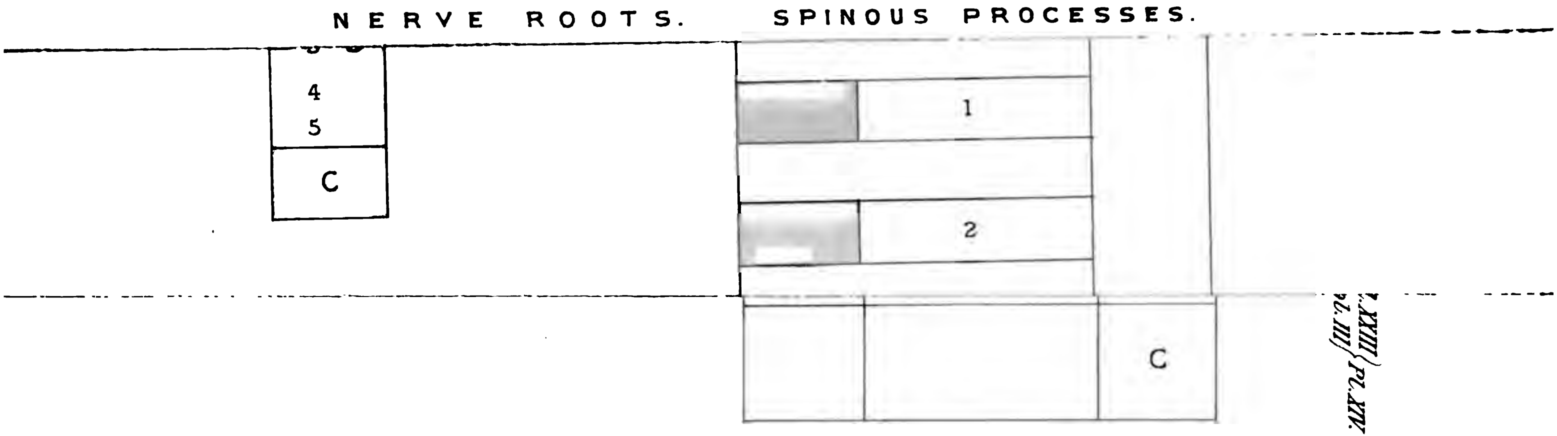


Chart showing the limits of the variations in the topographical relation between the superficial origins of the nerve roots from the spinal cord and the spinous processes of the vertebrae.

(Reduced one half.)

.XXIII} Pl. XIV.
l. III}

Fig. 1.

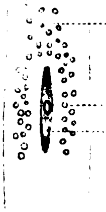


Fig. 2.

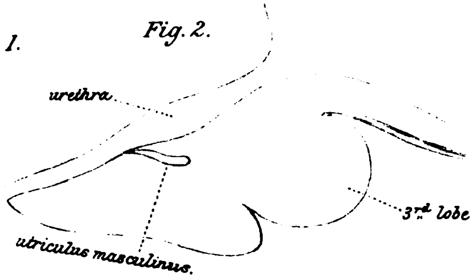


Fig. 3.

Fig. 4.

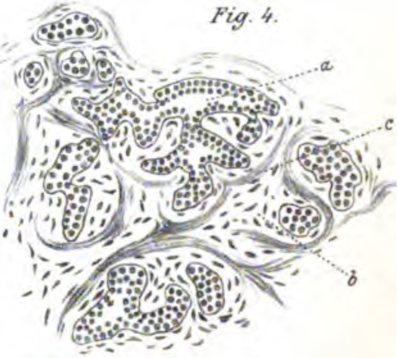
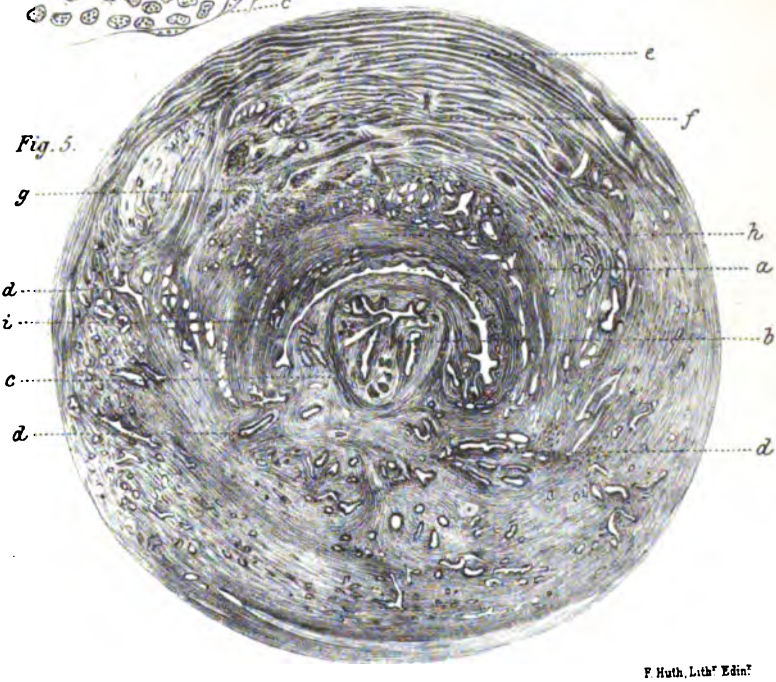


Fig. 5.



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PROSTATE GLAND.

PLATE XVI.

FIG. 1.

FIG. 2.

Permanent Photo. Valentine Blanchard & Lunn, Cambridge.

PLATE XVII.

FIG. 3.

Permanent Photo. *Valentine Blanchard & Lunn, Cambridge.*

PLATE XVIII.

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

Permanent Photo. *Valentine Blanchard & Lunn, Cambridge.*

PLATE XIX.

FIG. 8. FIG. 9.

FIG. 10.

FIG. 11.

FIG. 12. FIG. 13.

Permanent Photo. *Valentine Blanchard & Lunn, Cambridge.*

Fig. 3.

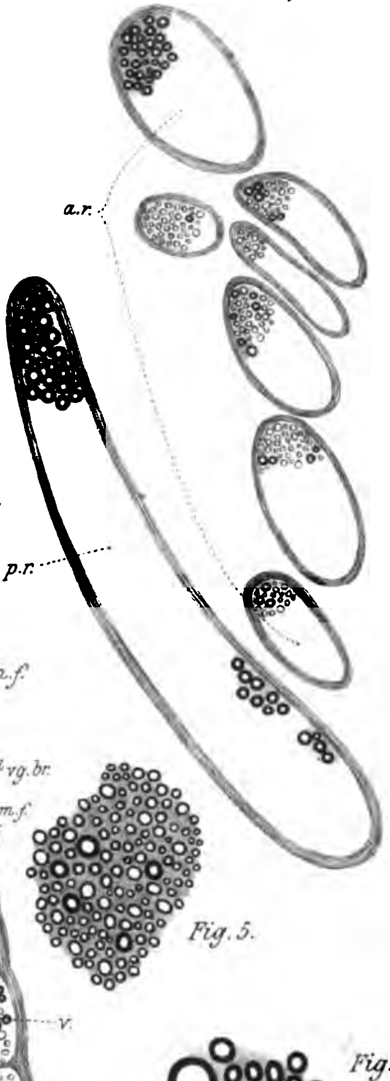


Fig. 2.

Fig. 6.

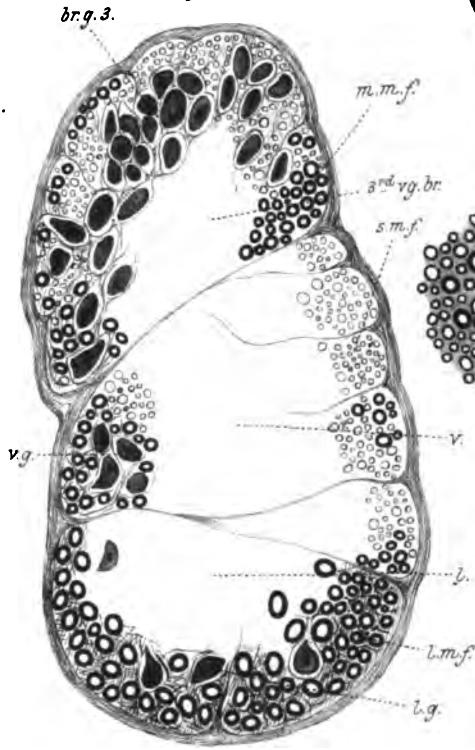


Fig. 5.

Fig. 4.

F. Huth, Lith^r Edin^r

VAGUS OF SKATE.

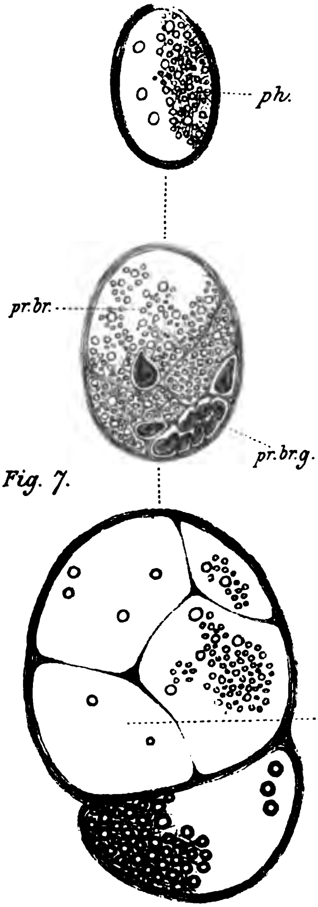


Fig. 7.

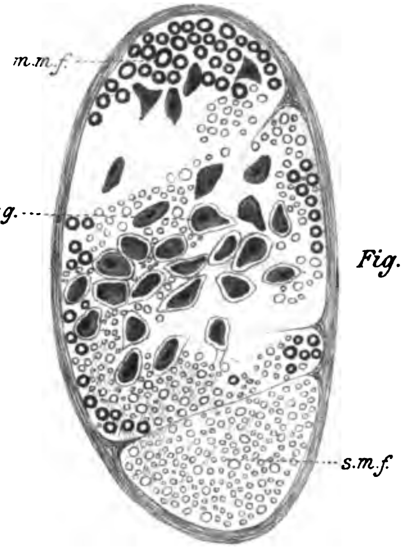
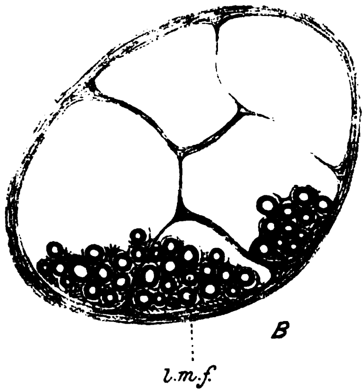


Fig. 8.



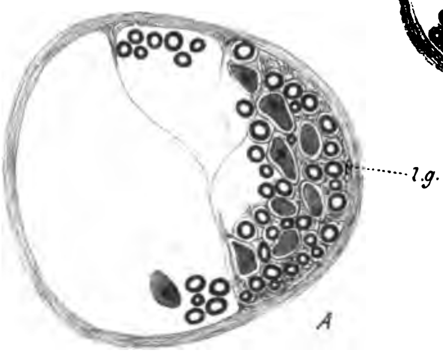


Fig. 9.

F. Huth, Lith.r Edin.r

VAGUS OF SKATE.

Journal of Anatomy and Physiology.

THE DEVELOPMENT OF DIARTHRODIAL JOINTS IN BIRDS AND MAMMALS.

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(From the Embryological Laboratory, University of Edinburgh.)

I. THE number and importance of the pathological conditions which affect joints and necessitate surgical interference have led to careful study of their normal and morbid anatomy, both macroscopic and microscopic. A considerable amount of attention has also been devoted to the investigation of their development, but yet the literature of this subject leaves many blanks in our knowledge, and there are many details in connection with the development of joints, from the period at which they first indicate their presence in the young embryo until they arrive at their permanent form, which have not been clearly elucidated.

II. *Summary of Recent Literature.*

Summarising the present state of our information regarding the development of joints from the recent literature on the subject, we find that, in the last edition of Quain's *Anatomy*, Dr Allen Thomson makes the following statement:[2]—

There are at first no joint-cavities, and the fibrous or connective tissue forming a sort of articular plate between the bone-matrices may therefore be said to unite them by syndesmosis. But very soon, or in the human embryo of from seven to eight weeks, when chondrification is complete, narrow slits make their appearance in the place

[1] Read to the Royal Society of Edinburgh, May 20, 1889.

[2] Quain's *Anatomy*, 9th ed., 1882, vol. ii. p. 886.

of the future joint-cavities, and the fibrous structures retiring from the interior towards the surface, the cavities undergo enlargement into their permanent form.

As the result of their study of the phalanges, Henke and Reyher[1] came to the following conclusions:—

The phalanges are added one after the other. When one of these pieces has reached a certain length, it becomes separated off by a transverse plate of somewhat differently condensed tissue . . . . . before the following piece is formed. This can be termed a *syndesmosis*, or at any rate can very well be compared with such. From this can now directly proceed a diarthrosis, when the interdisc thins and disappears, and so the two parts come into direct contact. Then in course of time these are transformed into polished cartilaginous surfaces in permanent contact. But since at this stage there is not much difference in size between the two surfaces, the joint is termed an *amphiarthrosis*. While they cannot assert that this development of a syndesmosis into an amphiarthrosis is general, yet they regard the stage of amphiarthrosis as one occurring in every diarthrodial joint, and forming the starting-point for its further development. Histologically, in five to six weeks' embryos (18–20 mm.), they described the transverse plate separating the phalanges from each other under the name of the *yellow disc*, picro-carmine being the staining agent employed. Further up the limb this yellow disc was replaced by discs staining darker yellow, but otherwise having the same general characters. These darkly-stained discs consisted of rows of small close-set cells, without intercellular substance. Moreover, the cartilage cells were not sharply separated from the small marginal cells, but transition occurs. At the end of the second month ($3\frac{3}{4}$–$4\frac{1}{4}$ cm.) the cartilages are still united by an interzone of small-celled tissue corresponding in position to the yellow disc of the earlier stage, but as yet there is no joint-cavity. At the beginning of the third month they describe the "interzone" becoming thinner in the axis of the limb until the axial portion is no longer present, but cartilage touches cartilage. The cartilage cells are sparingly embedded in hyaline intercellular substance, and where they reach the surface they are flattened. The genesis of synovial folds out of the interzone is indicated in the fourth and fifth months. In six months' embryos there can be seen appearances pointing to a weak synovial tissue passing between the articular surfaces. This has, however, never any tissue continuity with the joint-cartilage.

Bernays[2] speaks of a perichondrial layer of cells at whose cost the cartilage grows, and he terms it a "chondrogenous layer." He recognises the fact that, in addition to this, a band of tissue, consisting of round elements, may separate the abutting ends of two skeletal parts,

[1] Henke and Reyher, "Studien über die Entwickl. der Extremitäten des Menschen insbesond. der Gelenkflächen," *Sitzungsb. Wien. Akad.*, Bd. lxx. Abth. iii. pp. 217–273, 1874.

[2] Bernays, A., "Entwickl. d. Kniegelenks," &c., *Morph. Jahrb.*, Bd. iv.

while establishing tissue continuity. He first finds a joint-cavity in a human embryo of 4·5 cm., and states that it forms by a separation of the ends of the cartilages, between which there no longer exists any formative tissue. This dehiscence he ascribes to muscle contraction. He concludes that the capsule, menisci, interarticular ligaments, and synovial membrane are developed out of the indifferent tissue, found partly between the joint ends and partly around them. Further, he states that the inner surface of the synovial membrane is not clothed by any epithelial formation.

In a recent paper by Messrs Howes and Davies,[1] in which they discuss the "Morphology and Genesis of Supernumerary Phalanges," especially in Amphibia, they describe a syndesmosis from *Proteus*, and state that "such differences as are met with between the corpuscles of the epiphyses and of the syndesmosis are seen to be entirely due to pressure under apposition of the first named." In referring to another specimen, *Hyla arborea*, they conclude "that the phalanges and syndesmosis are, together with their investing sheath, differentiations of a continuous and common blastema; and that the syndesmosis, while intimately related to the sheath, are formed, not as ingrowths of the same, but as differentiations of that mass from which the phalanges are derived, and that they differ from these, initially, only in degree of elongation."

Lastly, Hertwig,[2] in describing the development of a joint-cavity, says:—

When, after the disappearance of the inter-tissue, the terminal surfaces of the developing cartilage come to directly touch, there appears between them a narrow fissure, the first foundation of the joint-cavity. There then gradually takes place a sharper delimitation of the cavity from the surrounding connective tissue by the development from one cartilage to the other of a firmer connective-tissue layer, which becomes the capsular ligament.

He refers to deviations in this method produced by complete and incomplete interarticular fibro-cartilages, which he regards as developed from the inter-tissue. In the former there arises a simple joint-cavity, where the cartilages are in contact, but this cavity becomes double where the cartilages are not in apposition; in the latter, there develops a joint-cavity, which is separated into two portions by an interdisc.

III. In the present inquiry I have studied the subject with special reference to diarthrodial joints, since they are the most elaborate as well as the most highly-developed of the varieties of articulations.

[1] Howes and Davies, *Proc. Zool. Soc. Lond.*, 1888.

[2] Hertwig, *Lehrbuch d. Entwicklungsgeschichte*, Th. ii., 1888, pp. 480, 481.

The characteristic features of fully-formed diarthrodial joints are—

1. The *complete cavity* which separates the opposing ends of the articulating surfaces from each other.
2. The *articular cartilage* which encrusts these free surfaces.
3. The *capsular ligament* enclosing the cavity and articular surfaces.
4. The synovial membrane lining the cavity.

In the adult joint the synovial membrane lines the internal surface of the capsular ligament, and may be likened to a cylinder open at each end. According to Toynbee,[1] it extends over the surface of the fœtal and adult articular cartilages, but differs from the reflex synovial membrane in being non-secretory and devoid of an epithelial layer. This view is not now accepted as regards adult articular cartilage, although a synovial membrane is still described as covering the fœtal articular cartilages, which are denuded of this membrane by the friction which follows the movements of the joints after birth.

Directing our attention, in the first place, to the articular cartilage, we observe that it never extends beyond the line of attachment of the synovial membrane. It consists of hyaline cartilage, and does not undergo ossification, although in its deeper parts a deposit of calcareous granules may be found. At its margin, cells with processes such as are characteristic of connective-tissue corpuscles are prolonged into it for a short distance from the synovial membrane. It is between the calcified zone, lying next the bone, and the free surface of the cartilage that we see evidence of cell-proliferation and active growth. Here the cells are arranged in short rows, placed vertically to the surface. As they approach the surface they become more irregular, until ultimately they lie parallel to and form the surface, presenting something of a stratified arrangement. Here and there vascular loops project a little way from the osseous tissue into the calcified zone, and the blood-vessels of the synovial membrane are also continued for a short distance over its marginal surface.

An examination of these facts appears to me to indicate that a close relationship, as regards their origin, exists between the

[1] Toynbee, *Lond. Jour. Med.*, 1849, i. p. 217.

articular cartilages, the fibrous capsule, and the synovial membrane. Moreover, I hope to show in what follows, that, developmentally, those different structures are derived from the same source, and that the "articular plate between the bone-matrices" is a cellular structure, as pointed out by Henke and Reyher,[1] and not a fibrous structure, as stated in Quain;[2] and that, in the midst of this mass of embryonic mesoblast, the joint-cavity appears, while from it are developed the articular cartilages, the capsular ligament, the synovial membrane, and any interarticular ligaments and fibro-cartilages which may be found in special articulations.

IV. The material used in the present investigation has been selected partly from birds and partly from mammals. The bird chosen was the Common Chick, as being most readily available. The limbs of the chick have been examined at the end of the 4th, 5th, 9th days, middle of 2nd week, 15th and 19th days of incubation, and those of the Black-headed Gull on the day of hatching.

Of mammalian embryos, the feet of the Mouse have been examined, when the embryo measured 14 mm. and 16 mm. nuchal length (nucho-caudal), as well as the feet of embryo rabbits of twenty-one and twenty-six days' gestation, and the phalanges of a young *human* embryo approaching the full period of utero-gestation.

In preparing the material for the microscope, part of the chick embryos have been hardened in picro-sulphuric acid and part in nitric acid of the ordinary strengths used for such purposes. The mammalian embryos have been hardened in nitric acid (5 per cent. sol.). Thereafter the embryos were partially dehydrated by alcoholic solutions of increasing strength up to 70 per cent. They were then stained in borax-carmine, and finally completely dehydrated by absolute alcohol. From this they were transferred to paraffin, through chloroform or benzol, and the sections were cut by the Cambridge rocking microtome. The thickness of the sections is ·006 mm.

I cannot sufficiently express my indebtedness to Mr George Brook, Lecturer on Embryology in the University of Edinburgh, in whose laboratory and under whose guidance the present investigation has been conducted.

[1] Henke and Reyher, *loc. cit.* [2] Quain, *loc. cit.*

V. *Description of the Sections.*

A. Birds.

At the end of the fourth day of incubation the wing of the chick measures ·8 mm., and in longitudinal sections it presents the form of a conical bulb which, when magnified 90 diameters, is seen to consist of a mass of mesoblast enveloped in a covering of epiblast. The cells of the epiblast are most numerous at the free end of the limb, where they form a kind of cap. The cells of the mesoblast core are closely packed together, most of them being spheroidal, with spherical nuclei in their interior. The cell substance does not readily absorb the staining agent (borax-carmine), and hence it is scarcely visible. The nuclei, however, stain deeply, and their outlines are very distinct. In all of them there is evidence of great activity, and every nucleus contains several nucleoli, three or four being quite frequent. There is no evidence of differentiation into special structures.

In horizontal sections of the hind limb made at the end of the fifth day of incubation, the free end of the limb has assumed a bulbous appearance (fig. 1). Examined under a magnifying power of 20 diameters, the majority of the mesoblast cells are still spheroidal and nucleated, but we find clear indications of a cell substance, because it retains the staining fluid, and the nuclei do not appear so isolated as they formerly did. Along the lines, where the cells come in contact, the contiguous surfaces are flattened, and these lines of contact are rendered visible by the staining agent, so that the section appears pervaded by a fine network. Spaces are also found in which numbers of cells are collected together. The nuclei of these cells stain very distinctly with the borax-carmine, but the surrounding cell substance is clear, and its outline often difficult to distinguish, although here and there it may be seen drawn out into long processes stretching to the walls of the space, which is probably the commencement of a vascular channel.

Along certain lines, which seem to presage the position of bone-matrices, the cells are much more closely packed together, and the margins of this collection of cells are quite distinctly localised, by deeper staining, from the surrounding spheroidal cells of the mesoblast.

Under a higher magnifying power—360 diameters (fig. 2)—the cells of the condensed and more open portions do not differ appreciably from each other, with the exception of the modified outlines consequent on closer packing. It must be noted, however, that the cell substance of the denser parts stains uniformly and faintly, giving it the appearance of being very finely granular, and imparting a firmer consistence than is visible in the more open parts of the section. Whatever structures, therefore, may ultimately be developed from these condensed portions of mesoblast, we are justified in stating that they are differentiations of a common and continuous blastema.

As growth proceeds the limb gradually elongates, and digits emerge from the bulbous extremity. If we examine the digits of a chick of nine days' incubation, we may see a process of differentiation affecting the cells of the condensed portions. In this process the granular cell substance surrounding the nucleus either secretes a translucent material or is transformed into this material. At any rate, we find that only a small amount of granular matter remains around the nucleus, while the cell is encapsuled in a hyaline matrix. In this manner cylindrical rods of cartilage are laid down as the primitive bone-matrices As noted by Henke and Reyher,[1]—an observation I am able to confirm,—these cartilaginous rods are developed in succession from the proximal towards the distal part of the limb. The rods are separated from each other by intervening masses of undifferentiated mesoblast cells which occupy the interval between the contiguous ends of two rods (fig. 3). The axial length of this articular plate is much less than that of the cartilages it unites together. Considered as an articulation, it may be compared with a syndesmosis, and the "articular plate' or disc consists of undifferentiated mesoblast cells, a fact also noted by Henke and Reyher,[2] who described them as without intercellular substance. At first there is no abrupt line of demarcation between the circumference of the disc and the general mesoblast by which it is surrounded, but on its proximal and distal aspects the cells of the bone-matrices show a tendency to become flattened in the transverse direction,—an appearance which affords a plane of demarcation between the bone-matrices

[1] *Loc. cit.* [2] *Loc. cit.*

and the articular disc as well as a future guide to the original limits of these structures. On the distal aspect of the articular disc the change from spheroidal mesoblast cell to flattened cartilage cell with a clear matrix surrounding it, is very abrupt, although here and there a round cell may project between two flat ones. On the proximal surface of the disc, the flattening of the cartilage cells is not so pronounced, but still there is a distinct difference between the structure of the disc and that of the bone-matrix. There is, of course, no sharp line of transition, since both are differentiations of a continuous and common blastema. These changes may be well seen in connection with the terminal phalanx of the digit of a chick of nine days' incubation. In the proximal articulations of the same digit the appearances are more advanced, for along the circumference of the articular disc the cells have undergone slight elongation in the axial direction of the limb, and thereby a differentiation is effected between the articular disc and the surrounding mesoblast. We now see that the articular disc projects a little distance beyond the margins of the cartilage rods, and also embraces their contiguous ends.

The next important change is the appearance of the cleft which forms the primitive joint-cavity. This may be seen in longitudinal sections of the wing of the chick at the end of nine days' incubation (fig. 4). As the cleft begins to make its appearance across the middle of the cellular articular disc, it proceeds from the periphery towards the centre, but without implicating the circumference of the disc. Gradually the cleft extends towards the axis of the disc, increasing in depth until the disc is finally divided into two portions, with the exception of its circumference, which is bounded by the slightly elongated cells corresponding in position with the future capsule of the joint.

This observation differs materially from the statements of Henke and Reyher,[1] as well as of Hertwig.[2] According to the former, the articular disc becomes thinner in the axis of the limb until the axial portion is no longer present, while the latter says that the joint-cavity appears after the developing cartilages come directly into contact owing to the disappearance of the inter-tissue.

[1] *Loc. cit.* [2] *Loc. cit.*

In support of my interpretation of the sections I have examined, fig. 5 (taken from the leg of the chick at the middle of second week of incubation) shows an interarticular ligament passing between the cartilages in the axis of the limb, a proof that the process of cleavage commences at the periphery and does not always extend across the centre of the articular disc, as well as a proof that the cleft is formed before the cartilages touch each other. Moreover, Hertwig admits that interarticular fibro-cartilages are developed from the articular disc, and therefore, when a complete meniscus is present, the joint-cavity must be formed without the articular cartilages coming in contact.

From what I have seen I am led to believe that the joint-cavity is first visible as a narrow fissure situated among the cells of the articular disc, when as yet the process of chondrification is at some distance from this cleft. Again, the process of cleavage, as already shown, does not always extend across the axis of the disc, a fact which is noted by Howes and Davies[1] in connection with *Nototrema marsupiatum*. With regard to interarticular fibro-cartilages, my observations point to the presence of two clefts which remain separate when a complete meniscus is found, but which merge with each other in the axis of the articular disc when an incomplete meniscus is present.

Although the cells composing the articular disc are for the most part spheroidal, yet those which form the sides of the primitive joint-cavity are distinctly flattened. Thus we have reached a stage at which the bone-matrices are still held in apposition by the closely-packed and somewhat elongated cells forming the circumference of the articular disc. These cells constitute the basis of the future capsule, which, according to Hertwig,[2] is a development of connective tissue from one cartilage to the other. The contiguous extremities of the articular cartilages are capped by the proximal and distal segments of the articular disc, these portions being now separated from each other by a closed cavity, the sides of which are lined by a continuous layer of flattened cells.

One cannot help observing that even at this early stage the articular ends of the bone-matrices have undergone a certain

[1] *Loc. cit.* [2] *Loc. cit.*

amount of moulding sufficient to enable them to foreshadow their ultimate form. As Hertwig[1] has already pointed out, this occurs at a time where there can be no movement, the muscular system not being developed; therefore it is necessary to fall back on the principle of heredity in order to find an explanation of these appearances.

Passing on to an examination of the condition of the joint as seen in longitudinal sections of the long claw of the chick at the end of fifteen days' incubation, we find that the cavity of the joint is completely formed, and is everywhere lined by a continuous layer of flattened cells, prolonged alike over the free surfaces of the articulating extremities and the internal surfaces of the investing capsular ligament. The process of ossification may be seen in the shaft of the bone-matrix, which is invested by a fibrous perichondrium, except at the articular extremity, where we still find evidence of the original limit of the cartilaginous rod. The ossified cartilage presents rows of cells lying parallel to the long axis of the limb, the individual cells in these rows being elongated in the transverse direction. The whole arrangement indicates the first step towards the formation of primary medullary spaces.

It will be remembered that the articular disc, with the exception of its circumference, was divided into two portions by the joint-cavity, and that each portion formed a cap for the end of a cartilaginous rod. These segments of the articular disc have now undergone differentiation into cartilage, but the process has not yet affected its whole thickness, for there are still several rows of cells next to the cavity of the joint which have not completely undergone this transformation. These continue to stain deeply with borax-carmine, partly as the result of their close packing and partly owing to the very small amount of intercellular substance.

The undivided circumference of the articular disc can be seen directly continuous with the cartilaginous products derived from its two segments. In this part, which forms the rudiment of the capsular ligament, changes may be traced which result in the formation of the fibrous tissue. The spheroidal cells of which it was originally composed undergo elongation, the

[1] *Loc. cit.*

nuclei lose their spherical shape and lengthen out in the long axis of the cell. The cell substance becomes fibrillar and more translucent. Apparently they arrange themselves in bundles, running in various directions, for, at some parts of the section (fig. 7) rows of nuclei almost rectangular in outline may be seen. These rows run parallel to each other, but separated by wavy fibres; at other parts of the section, usually nearer to the joint-cavity, we find the nuclei lying closer together and presenting the appearance of bundles cut transversely. These features of the capsule may be traced towards the articular cartilage, and we observe that the nuclei, arranged in rows, pass by small gradations in shape into the form which is characteristic of the cartilage cell, while the fibrillar portions of the capsule pass insensibly into the hyaline cartilage. When an interarticular cartilage is present, it is continuous with the capsule, and a similar series of changes may be traced in it, whereby the original mesoblast cell is transformed into fully-formed fibrous tissue.

Carrying the observations a stage further, and examining the joints of a chick after nineteen days' incubation, we see the free surface of the articular cartilage covered by flattened cells (fig. 8). Beneath these there are two or three rows of cells not quite so flat as those on the surface, while still deeper the flat form of cell gives place to one more rounded. Nevertheless, with the exception of the layer of flattened cells on the free surface, they all appear to be cartilaginous, and only differ from each other in the amount of hyaline matrix which surrounds them. The flattened surface cells lie so close to the cavity of the joint that apparently they are not surrounded by hyaline substance. The further we proceed from the surface the more distinctly cartilaginous does the tissue become. The cells are irregularly disposed, and it is only when we reach the bone-matrix that we find the cells arranged in parallel rows, as already mentioned.

Although I am not in a position to make a definite statement on the point, yet there are many appearances which seem to indicate that the whole epiphyseal end of a bone is developed from the cells of the articular disc. In longitudinal sections taken from the long claw of the Black-headed Gull on the day of hatching, the joint-cavity presents appearances similar to those described above.

B. Mammals.

In this group my observations have principally been made on sections illustrating the early stages of the formation of the joint-cavity, since it is mainly in connection with this question that diversity of statement prevails. I have been particularly struck with the close similarity which exists between the appearances presented by the sections taken from early stages of joint formation in birds and in mammals, as a comparison of the plates will show. Fig. 9 is a drawing taken in longitudinal section of the hind-foot of an embryo Mouse of 14 mm. nuchal length, and examined under a magnifying power of 160 diameters. The bone-matrices are seen surrounded by closely-packed cells, fading gradually into the cartilage. The ends of the cartilage rods are separated from each other by a mass of spheroidal undifferentiated mesoblast cells, forming the articular disc and establishing tissue continuity between them. The circumference of the disc extends beyond the margins of the bone-matrices, and appears to envelop the distal end of the one cartilage to a greater extent than the proximal end of the other.

The distinction between the cartilage rods and the articular disc is emphasised by the deeper staining of the cells on the surface of the former, otherwise there is no apparent difference between these cells and those of the articular disc. Each cartilage cell is surrounded by a small area of hyaline substance, and the lines of junction of these areas have become stained, and are therefore visible.

Compared with fig. 3, the general similarity is very striking. The cells are larger in the Chick, and the crowding of cells on the surface of the cartilage is more marked in the Mouse. The moulding of the opposing ends of the cartilages is visible in both.

Fig. 10 is from a longitudinal section of the hind-foot of a Rabbit of twenty-one days' gestation, under a magnifying power of 120 diameters. Here the bone-matrices are still distinctly separated from each other by a mass of undifferentiated cells. Within this area the primitive joint-cavity is seen. Practically it is complete, but in the centre a few straggling cells are visible,

indicating the last point of cleavage. The cells which form the walls of the cleft are somewhat flatter than the rest. It will be noted that the cells are closely packed next to the cavity; and that they are traced to some distance before cartilage formation is established. The moulding of the ends of the bone-matrices is also observable. Compared with fig. 4, from the wing of the Chick, the close similarity is again noteworthy, and both seem to prove that the joint-cavity appears before and not after the disappearance of the articular disc (syn. inter-tissue), as stated by Hertwig[1] and Bernays.[2]

Judging from the fact that the appearances described correspond so closely with those observed in the Chick, there seems no reason to doubt that the fate of the articular disc in the case of mammals follows a course similar to that already noted in the Chick, and therefore I have not pursued the inquiry further in this direction, with the exception of an examination of the phalangeal articulations of a human fœtus approaching the full period of utero-gestation. Hitherto, in indicating the fate of the articular disc and the structures derived from it, I have not discussed the question of the synovial membrane. Toynbee's statement with regard to its presence on adult articular cartilage is not now accepted, and after a careful examination of a large number of sections I am inclined to doubt whether it be present as a covering for the articular cartilages prior to birth. It certainly seems strange that a specialised membrane should be developed, and that its first function should be to disappear under friction. Moreover, the synovial membrane lining the capsule of such a joint as the shoulder must of necessity also be subjected to much friction. Intracapsular tendons, interarticular ligaments and cartilages are constantly exposed to friction in the various movements of joints, and yet they do not lose their synovial coverings. It would be remarkable were the same cause to lead to loss of the synovial membrane lining one part of the joint-cavity while it left it unaffected at another.

Undoubtedly the joint-cavity is lined by cells of a flattened appearance practically from its very commencement. The absolute proof of a secreting membrane is its vascularity. If the articular cartilage of the Chick of nineteen days' incubation be

[1] *Loc. cit.* [2] *Loc. cit.*

subjected to examination under a high magnifying power (fig. 8, × 680), it will be obvious that there is no vascularity, and that flattened cells are not confined to the free surface of the articular cartilage, but are found in several rows underneath the surface. As the distance from the surface increases, so do the individual cells become rounder and the amount of hyaline material greater, until the cartilage formation is complete.

The appearances presented by longitudinal sections of the articular cartilage of the phalangeal articulation of the human fœtus approaching the full period of utero-gestation differ somewhat from those just described. Here (fig. 11) the free surface is no longer clothed by flattened cells, but in their place we find a narrow band devoid of cells, and staining somewhat more freely than the subjacent hyaline cartilage. From the soft and slightly-ragged character of the margin of this band, which is continuous with the flat cells lining the capsule, it would seem as if it represented the flattened cells which had disappeared by a process of degeneration. I am therefore of opinion that the flat cells on the free surface of the articular cartilage do not reach the stage of a specialised secreting membrane in either the bird or the mammal, and I would agree with Bernays[1] in considering them to be non-epithelial; while in the human fœtus they undergo a process of degeneration. With regard to those flat cells lining the capsule and covering interarticular structures, they are always readily accessible to a vascular supply, and may thus become specialised as a secreting structure.

Conclusions.

1. The bone-matrices and the articular disc possess a tissue continuity, and are derivatives of a common blastema, of which the articular disc is at first the undifferentiated form.

2. The articular disc may conduct itself as follows:—

(*a*) It may develop into a plate of cartilage, and form a *synchondrosis*, *e.g.*, the articulation between basi-occipital and basi-sphenoid bones.

(*b*) It may differentiate into fibrous tissue, and form a *syndesmosis* or *synarthrosis*.

(*c*) It may partly cleave, and form a *joint-cavity*.

[1] *Loc. cit.*

3. The joint-cavity appears within the articular disc at a period when the process of chondrification is at some distance from the cavity.

4. If the cavity remain of small size, and the surrounding articular disc develops into fibrous tissue, an *amphiarthrosis* is formed, *e.g.*, the joints between vertebral bodies. (This is specially well seen in some Cetacea, and probably the epiphyseal plates on the bodies of vertebræ are also derived from the articular disc.)

5. The cavity may enlarge to form a *diarthrosis*.

6. When the joint-cavity is single we have a simple diarthrosis. When the cleft is single, but does not extend across the axis of the disc, an interarticular ligament is formed. When there are two cavities we have a diarthrosis, with an interposed meniscus. When the two clefts unite in the centre, we have the condition seen in an incomplete meniscus.

7. The proximal and distal segments of the articular disc develop into the articular cartilages of the joint, and probably form part, if not all, of the epiphyseal ends of the bones.

8. The circumference of the articular disc develops into the capsule of the joint.

9. Interarticular fibro-cartilages and ligaments are derived from the articular disc as the result of the modifications of the joint-cavity.

10. The cells lining the joint-cavity have a double fate. Those in relation to the ligamentous structures, and thus within reach of a direct blood supply, become specialised into a synovial membrane. Those applied to the articular cartilage are present in the bird at the period of hatching; but in the case of the mammal they have undergone degeneration. Probably in both cases they disappear as the result of friction.

Pathology affords corroborative evidence of the derivatives of the articular disc, for the structures enumerated as being developed from it are simultaneously affected by pathological conditions.

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EXPLANATION OF PLATE XXII.

With the exception of the drawings given by Howes and Davies[1] in illustration of their paper already referred to, I have not been able to find any histological drawings of the development of joints. The accompanying series have been made with the assistance of Zeiss' camera lucida.

Fig. 1. H. S. of the hind limb of chick, end of fifth day of incubation. × 20.

Fig. 2. Enlarged view of fig. 1. × 360.

Fig. 3. L. S. of leg of a chick, ninth day. × 75, showing articular disc.

Fig. 4. L. S. of wing of chick, end of ninth day. × 75, showing joint-cavity.

Fig. 5. L. S. of leg of chick, middle of second week. × 75, showing interarticular ligament.

Fig. 6. L. S. of long claw of chick, end of nineteen days. × 20.

Fig. 7. Enlarged view of fig. 6. × 360, showing formation of fibrous capsule.

Fig. 8. Enlarged view of fig. 6. × 680, through articular cartilage.

Fig. 9. L. S. of hind foot of mouse, nuchal length 14 mm. × 160.

Fig. 10. L. S. of hind foot of rabbit, 21 days' gestation, showing joint-cavity. × 120.

Fig. 11. L. S. of phalangeal joint of human fœtus approaching full period of utero-gestation, showing free surface of articular cartilage. × 480.

[1] *Loc. cit.*

ON THE INNERVATION OF THE MUSCLES OF THE SOFT PALATE. By WILLIAM ALDREN TURNER, M.B. Edin.

As the subject of this paper is one on which some difference of opinion exists, the following case, which was under observation, may be of interest:[1]—

Case.—The patient was a young man, æt. 21; his habits were temperate, and there was nothing in his personal or family history deserving special mention. In September 1888 he noticed a small swelling in the upper part of his neck, on the right side. It grew slowly in size, and did not cause him any inconvenience, but he observed that he was losing flesh, and that the character of his voice was changing; he also suffered from occasional attacks of vomiting. The following was his condition when he came under observation in January 1889:—There was almost complete atrophy of the right sterno-cleido-mastoid muscle, the only part visible being its sternal attachment. The upper part of the right trapezius muscle was also atrophied; the head was turned as easily to the left as to the right side, but he could not shrug his right shoulder as well as his left. The tongue was protruded straight, but was more readily put into the left cheek than into the right; the right half was very much atrophied. On examining the back of the mouth, it was seen that while the palate was at rest, the right half of the velum was at a slightly lower level than the left; but on phonation, the right arch was immobile, while the left arch was drawn upwards and to the left; the uvula was not curved to either side. His voice was hoarse and low-pitched, and he coughed "like one whose trachea is open." On laryngoscopic examination the right vocal cord was seen to occupy the cadaveric position; there was anæsthesia of the right half of the larynx, and a large quantity of muco pus was collected about the folds of mucous membrane and the base of the tongue. There was loss of taste on the right posterior third of the tongue, and the vomiting reflex was in abeyance. There was slight narrowing of the right palpebral fissure from retraction of the right eyeball, and the right pupil was contracted. The optic discs were natural, and there was no difference in the size of the retinal vessels in the two eyes. His pulse was regular (72 per minute) and dicrotic; there was no heart murmur; the respirations were 24 per minute, and there were no signs of pulmonary disease. There was a slight trace of albumen in the urine, and his general health was good. In February the tumour

[1] I am indebted to Dr Andrew, physician to St Bartholomew's Hospital, for permission to refer to this case.

had grown considerably in size, and invaded the parotid gland, so that complete right facial paralysis ensued and hearing became defective, probably by occlusion of the right external auditory meatus from the growth of the tumour upwards. In March the patient's health began to fail, and there was no improvement in the paralytic symptoms, and in April he died exhausted. An autopsy was not obtained.

It was evident that several important cranial nerves were being more or less pressed upon by the tumour, which was probably a sarcoma. The new growth originated amongst the deep structures of the neck, and in its outward growth implicated the following nerves:—The outer branch of the right spinal accessory nerve; the right vagus and the inner branch of the spinal accessory, as was evidenced by paralysis of the right vocal cord, of the right side of the palate and the anæsthesia over the area of distribution of the right superior laryngeal nerve; the hypoglossal and glossopharyngeal nerves; the sympathetic nerve; and, later on, the portio dura.

English text-books on anatomy and physiology teach, probably as a result of the writings of Sir Charles Bell,[1] that the muscles of the soft palate receive their motor nerve-supply from the portio dura through the sphenopalatine ganglion and its posterior palatine branches; but it has long been held in Germany, and was first pointed out from clinical observation in this country by Dr Hughlings Jackson[2] in 1864, that the palatal muscles are supplied by one of the nerves arising from the medulla oblongata, probably the accessory nerve to the vagus. It may, therefore, not be unprofitable to review briefly the literature on the subject, and to bring forward evidence for or against one or other of the views held concerning the motor supply of the muscles of this region.

A. *Evidence in favour of the Portio Dura.*

a. Anatomical.—The small or posterior palatine nerve from the sphenopalatine ganglion was originally described by Meckel[3] as going to the levator palati and azygos uvulæ muscles; and

[1] *Philosophical Transactions*, 1821; and *Exposition of the Natural System of the Nerves of the Human Body*, London, 1824.

[2] *Lond. Hosp. Rep.*, vol. i., 1864.

[3] Meckel, *De quinto pare nervorum cerebri*, Göttingen, 1748.

according to Longet,[1] this nerve contains motor fibres for these muscles, which are derived from the portio dura through the great superficial petrosal and Vidian nerves.

b. Experimental.—The evidence on this point is not very satisfactory. Of five experiments upon dogs, Valentin[2] observed a slight movement of the soft palate in only one; and Debrou[3] made a similar observation in one of five experiments which he performed. Longet's own experiments confirm these, but for certain other reasons he holds that the soft palate is supplied by the portio dura.

c. Clinical.—Records of cases in which unilateral paralysis of the soft palate was associated with facial palsy are scattered throughout medical literature; but as many observers only noted the position of the uvula, it is doubtful whether real paralysis of the palate was present in many of the cases. Probably the first case of this association was one recorded by Montault[4] in 1831. Longet[5] quotes cases which he had himself seen, and in them the uvula pointed to the side opposite to the facial palsy. Alexander Shaw[6] directed attention to the fact that in facial palsy there may be a deflection of the uvula to the same side as the facial lesion. Romberg[7] also narrates four cases in which the uvula was deflected to the paralysed side. Trousseau[8] describes the uvula as being drawn to the sound side. Davaine,[9] however, noted a downward displacement of the velum palati on the paralysed side; and W. R. Sanders[10] describes four cases in which hemiplegia of the velum on the paralysed side and deflection of the uvula to the same side were present. In facial spasm, Schütz and Laube[11] have observed clonic contractions and drawing up of the uvula on the same side as the facial spasm.

[1] Longet, *Anatomie et Physiologie du Système Nerveux*, vol. ii., Paris, 1842.
[2] Valentin, *De functionibus nervorum cerebralium.*
[3] Debrou, *Thèse Inaug.*, 1841, quoted by Longet.
[4] Montault, *Thèse Inaug.*, 1831.
[5] Longet, *op. supra cit.*
[6] Shaw, *Med. Gaz.*, Sept. 1837.
[7] Romberg, "Diseases of Nerv. Syst.," *Syd. Soc. Trans.*
[8] Trousseau, *Clinical Medicine.*
[9] Davaine, *Gazette Medicale*, quoted by Sanders.
[10] Sanders, *Edin. Med. Jour.*, Aug. 1865.
[11] Quoted by Gowers, *Nervous System*, vol. ii. p. 233.

B. *Evidence against the Portio Dura.*

a. The experiments of Valentin and Debrou cited above may be regarded as evidence against, rather than in favour of, this nerve, and they are confirmed by the observations of Volkmann[1] and Hein.[2] John Reid's[3] experiments upon dogs failed to convince him that any of the muscles of the soft palate were supplied by the seventh nerve; while Messrs Horsley and Beevor,[4] in their experiments upon monkeys, were unable to produce contraction in the muscles of the soft palate by stimulating the portio dura within the cranial cavity. Valentin,[5] further, in fifteen experiments failed to excite movements of the palate by irritation of the great superficial petrosal nerve.

b. Clinical evidence tends to confirm the results of these experiments; but it may be well to inquire what are the physical signs of unilateral paralysis of the palate, as there is considerable difference of opinion on this point.

In paralysis of the right side of the palate, the physical signs are, when at rest, a lowered and less arched condition of the right side of the velum; on phonation, elevation of the left side of the velum, with heightening of the left arch and a lax state of the right arch. The position of the uvula is of no clinical value; in health it is very often curved to one or other side, so that in estimating the condition of the palate in a suspected case of paralysis, the position of the uvula is best left out of account.

It had long been known that paralysis of the face, due to disease of the seventh nerve, is sometimes associated with corresponding paralysis of the soft palate. But Todd and Bowman[6] in 1856 pointed out

"that paralysis of the velum pendulum palati on the same side as the palsy of the face sometimes accompanies the other signs of this form of palsy cannot be doubted, but the frequency of its absence is sufficient to denote the trifling influence of the nerve upon the palatine muscles."

[1] Volkmann, *Müller's Archiv Jahrg.*, 1840, s. 485.
[2] Hein, *Müller's Archiv Jahrg.*, 1844.
[3] Reid, *Physiological, Pathological, and Anatomical Researches*, Edin., 1849.
[4] Horsley and Beevor, *Proc. Roy. Soc.*, vol. xliv., 1888.
[5] Valentin, quoted by Todd and Bowman.
[6] Todd and Bowman, *Physiological Anatomy*, 1856.

Dr Hughlings Jackson,[1] in 1864, stated that he had never seen paralysis of the palate due to disease of the facial nerve, and he adds—

> In cases even of paralysis of this nerve, from disease of the pons Varolii, the palate has seemed to be quite normal; real paralysis of the palate is decidedly a rare thing; if we exclude diphtheritic paralysis, it is very rare indeed;

and Dr Gowers[2] says he has noted the condition of the palate in more than a hundred cases of facial paralysis due to disease of the nerve in various situations, and found in only one of them evidence of paralysis of the palate, and this was on the side opposite to the palsy of the face. Further, if the palate was innervated through Meckel's ganglion, in cases where this structure had been excised palsy of the palate on the same side ought to ensue; but Dr Bastian[3] records a case where this operation had been performed, and in which he observed that the palate was quite symmetrical and its mobility not in the least impaired. In a case of facial spasm,[4] where the autopsy showed an aneurism of the left vertebral artery pressing upon the portio dura, no spasm of the palate was observed.

C. *Evidence in favour of the Accessory Nerve to the Vagus.*

a. Anatomical.—Luschka and Henle[5] originally described nerve filaments which passed from the pharyngeal plexus to some of the muscles of the soft palate, this plexus being formed of branches from the glossopharyngeal, vagus, accessory to vagus, and sympathetic nerves.

b. Experimental.—John Reid,[6] in 1849, produced movements in the pharynx, velum pendulum palati, larynx, and œsophagus when he stimulated the roots of the pneumogastric nerve of a dog; Volkmann in a similar manner excited movements of the superior and inferior constrictors of the pharynx and of the levator palati, azygos uvulæ, palato-pharyngeus, crico-thyroid,

[1] Hughlings Jackson, *loc. supra cit.*
[2] Gowers, *Diseases of Nerv. System*, vol. ii. p. 218.
[3] Bastian, *Paralysis, Cerebral, Bulbar, and Spinal*, p. 446.
[4] Recorded by Schultze and quoted by Gowers, *op. supra cit.*, p. 230.
[5] Henle's *Handbuch der Anatomie*, Bd. iii. p. 436, Edin., 1868.
[6] John Reid, *loc. supra cit.*

arytenoid, and œsophageal muscles; Hein,[1] who restricted his observations to the palate, observed contraction of the levator palati, azygos, uvulæ, and palato-pharyngeus muscles. In 1842 Bischoff[2] stated that he had obtained movement of the velum pendulum, in which contraction of the levator palati was very decided, when he irritated the root either of the vagus or its accessory nerve. Stilling, Wagner, and Claude Bernard confirm these experiments. Messrs Beevor and Horsley[3] obtained movements of the levator palati muscle when the nervus accessorius vagi was stimulated within the cranial cavity of a monkey. From these experiments it appears that motor fibres for the muscles of the soft palate are derived through either the vagus or its accessory nerve. In 1838 John Reid[4] had exposed the pharyngeal branch of the vagus in a dog and irritated it, and observed "vigorous movements of the constrictors of the pharynx, stylo-pharyngeus muscle, and muscles of the soft palate;" he therefore regarded the nerve as motor for these muscles. It would seem, therefore, that the muscles of the soft palate derive their motor supply from the pharyngeal plexus through the pharyngeal branch of the vagus, and that this nerve obtains its motor fibres from the accessory nerve to the vagus.

c. Clinical.—In 1864 Dr Hughlings Jackson[5] showed, from a series of cases which had been under his observation, that in disease affecting the nuclei or the roots of the nerves, arising from the medulla oblongata (glossopharyngeus, vagus, hypoglossus, and nervus accessorius vagi), paralysis of the soft palate, either unilateral or bilateral, was a constant sign; and that with it, but by no mere random association, there was paralysis of one or both halves of the tongue and of one or both vocal cords. Since these cases were recorded, numerous instances of the association of these paralyses have been observed.[6]

But cases in which a visible and palpable tumour has caused

[1] Hein, *Müller's Archiv Jahrg.*, 1844.

[2] Bischoff, *Müller's Archiv Jahrg.*, 1843.

[3] Beevor and Horsley, *loc. supra cit.*

[4] Reid, *Edin. Med. and Surg. Jour.*, 1838.

[5] Jackson, *loc. supra cit.*

[6] *E.g.*, *Lond. Hosp. Reps.*, vol. iv.; Mackenzie, *Brit. Med. Jour.*, Mar. 1883; Broadbent, *Med. Soc. Trans.*, 1882.

similar signs seem to be of rarer occurrence. Dr Macbride[1] has recorded a case in many respects similar to the one narrated at the commencement of this paper. In his case, although the tongue was protruded to the paralysed side, there was no atrophy, and there was no involvement of the sympathetic nerve. In another case recorded by Frænkel,[2] in addition to the signs already described, there was a very rapid action of the heart. A very interesting case is mentioned by Romberg,[3] as having been recorded by Gendrin, in which there was atrophy of the left half of the tongue, with great diminution of the sense of taste, weakness of the left side of the body, aphonia, and difficulty in swallowing, but with no loss of sensation on the left side of the tongue. The autopsy revealed a hydatid cyst pressing on the left hypoglossus, vagus, and glossopharyngeus; there was also atrophy of the muscles of the left half of the pharynx and velum pendulum palati. The condition of this latter structure did not appear to have been examined during life. Other similar cases have been recorded by Dufour and Tuerk, Gerhardt and Scheck.[4]

The great bulk of the evidence, therefore, is in favour of the accessory nerve to the vagus being the motor nerve to the muscles of the soft palate as well as to the vocal cords, and the course of the fibres is simple. The nucleus of origin of the accessory nerve is in very intimate connection with the nucleus of the hypoglossus, so that disease which affects the origin of one nerve will in all probability involve the other; there thus arises the associated paralyses of the tongue, soft palate, and vocal cords. If paralysis of the soft palate exist either on one or both sides, the larynx ought to be examined and the disease sought for, not in connection with the facial nerve but with the vagus and its accessory nerve.

There only remains to be considered the motor supply of the tensor or circumflexus palati muscle. This is commonly stated to be derived from the motor division of the trigeminus. The accuracy of this statement may be doubted. I have been unable to find a single recorded case in which disease of this nerve was

[1] Macbride, *Ed. Med. Jour.*, July 1885.
[2] Frænkel, *Berl. Klin. Wochens.*, No. 3, 1875, quoted by Macbride.
[3] Romberg, *Syd. Soc. Trans.*, vol. ii. [4] Quoted by Macbride.

associated with paralysis of the tensor palati muscle, which theoretically would be shown by a dragging of the raphé to the non-paralysed side.

Sir Charles Bell,[1] who records many cases of disease of this nerve, does not mention the condition of the palate in any of them. Romberg[2] never saw paralysis of the tensor palati associated with disease of the motor division of the fifth nerve; and Dr Gowers[3] holds the same opinion. Experimental evidence also is not of a satisfactory nature. John Reid[4] failed to elicit palatal movement on irritating the motor division of the trigeminal nerve; and Longet[5] does not mention any effect on the palate when this nerve was stimulated.

It is therefore probable that the tensor palati muscle receives its motor supply from one of the bulbar nerves, and that its centre is similar or nearly related to that for the levator palati muscle, for in chronic bulbar paralysis, not only is the movement of elevation in abeyance, but the palatal curtain hangs loose and flaccid. If the tensor palati muscle is not innervated through the pharyngeal plexus, the following is a possible course for the motor nerve filaments:—They leave the medulla by the accessory nerve and join the vagus; from this they pass to the glossopharyngeus by communicating branches, and, entering the tympanic branch, are conveyed to the small superficial petrosal nerve, so as to reach the otic ganglion, and from this be distributed to the muscle. This is a circuitous route, but not more so than that taken by the fibres subserving the sense of taste on the anterior two-thirds of the tongue.

Summary.—From the preceding the following general conclusions may be drawn:—

1. That there is not sufficient experimental or clinical evidence to support the doctrine that the muscles of the soft palate are supplied by the portio dura.

2. That experimental evidence shows that these muscles are innervated by the internal branch of the spinal accessory (nervus accessorius vagi), whose fibres are distributed along with certain branches of the vagus.

[1] Bell, *The Nervous System of Human Body*, Edin., 1836.
[2] Romberg, *op. supra cit.*
[3] Gowers, *op. supra cit.*, p. 202.
[4] Reid, *op. supra cit.*
[5] Longet, *op. supra cit.*

3. That sufficient clinical evidence exists to prove that paralysis of the palate results from disease affecting the medullary centre, the roots and the peripheral distribution of the vagus and its accessory nerve.

4. That with the paralysis of the palate (palatoplegia) there is associated paralysis of the tongue (glossoplegia) and of the vocal cords (laryngoplegia), either unilateral or bilateral, according to the situation of the disease.

ABSENT THORACIC DUCT CAUSING ŒDEMA OF A FŒTUS.

By ALFRED J. SMITH, M.B., *Assistant Master, Rotunda Hospital, and* AMBROSE BIRMINGHAM, M.B., *Professor of Anatomy, Catholic University, Ireland.*
(PLATE XXIII.)

THE absence, so far as we can find, of a record of a similar condition, leads us to hope that the following case may be of interest, not only from an anatomical but also from a pathological point of view. It is a case in which that peculiar and rare condition known as œdematous fœtus, the causation of which has up to the present been virtually unknown, was found to depend upon absence of the thoracic duct, lymphatic glands, and lymphatic trunks generally.

First, as to the frequency of general œdema of the fœtus the recorded examples are few. Professor Delamotte's case in 1765 is apparently the first. Keiller, Betscher, Steinwerker, Lawson Tait and others describe cases in which this condition was found, and each of the three latter has brought forward a theory to account for the production of the abnormal state. Betscher believed that the œdema was due to an obstacle in the umbilical blood-vessels; Steinwerker looked upon it as elephantiasis congenita cystica; while Lawson Tait advances the theory of stenosis of the foramen ovale. That none of these is a satisfactory explanation of the production of this peculiar condition we are led to believe; at least none of them was present in our case, while a much more evident and rational cause was found, and a cause which apparently was not sought for in any of the other cases.

The œdematous fœtus, the subject of this paper, was one of a pair of twins, both males, which were prematurely born, in the twentieth week, of a healthy mother, with a good family history. One of the twins was perfectly normal, and in our examination of the abnormal one we found comparison with the healthy fœtus the greatest assistance. The appearance of the abnormal fœtus was peculiar in the extreme; it was about three times as large as its healthy brother, and it bore a most striking resemblance to two large tomatos strung together, one being repre-

sented by the head, the other by the body, and this resemblance was enhanced by the peculiar pinkish colour of the skin. The scalp was so much distended that the bones of the cranium could nowhere be felt, and the integument over the entire body so tense that it did not seem possible to bend the limb without running the risk of bursting the skin. There was no pitting on pressure; on puncture, a glairy fluid like white of egg escaped. The head was extremely large, and was made up of a number of puffy swellings, separated by deep sulci (see fig. C); on the anterior aspect were two bulgings on each side, in addition there was a large one above, extending from the nose over the head, and a small one below the chin. The nose, the mouth, and the chin, which were well formed, were almost completely buried beneath these overhanging eminences. From the round pimple-like nose there ran outwards and upwards on each side a deep sulcus, which bifurcated about three-eighths of an inch from the nose into branches, one of which ran upwards and outwards, the other downwards and outwards; another deep sulcus ran down from the nose on each side close to the middle line and parallel to its fellow of the opposite side, separating the nose, mouth, and chin from the distended cheeks. These sulci were natural depressions, which were made sulci, sometimes half an inch in depth, by the enormous œdematous distension of the subcutaneous tissue in the intervals between the depressions. On the surface, even upon going to the bottom of the sulci, no trace of an eye or eyelids could be found; on dissection a well-developed eye was discovered underlying the point of bifurcation of the fissure which runs upwards and outwards from the nose, not under the rounded prominence in the angle between its branches, as might be expected (see fig. C).

The subcutaneous tissue was œdematous to such a marked degree that in parts it was three-fourths of an inch in depth, while the subcutaneous tissue in the healthy twin brother was only about $\frac{1}{50}$th of an inch in thickness. The muscles, and the other tissues of the body which contain much areolar tissue, were also markedly œdematous. This was the condition noted upon first observation, before a complete examination was made.

Bearing upon the case we found the following statements:—(1) Dareste, while making experimental researches on the production of monsters, found as a consequence of arrested development of the vascular spaces, that the blood corpuscles remained imprisoned in the cavities where they were formed, and that a general dropsy followed, with a marked accumulation of fluid in the tube that forms the spinal cord and the cephalic vesicles. (2) Professor Franks states that he has found hydrops occurring in the bovine species, due to a complete absence of the thoracic duct and the mesenteric glands.

Thinking that this latter might have something to do with the production of the œdema in our case, we first examined the thorax of the normal twin, and immediately found the thoracic duct in its usual position, and lower down we found in the abdomen mesenteric glands present in abundance (see fig. A). Next we opened the thorax of the œdematous fœtus and sought the thoracic duct with the greatest care in its usual position, but failed to find it there. We next examined the junction of internal jugular and subclavian veins on both sides with negative results; in fine, we searched every part of the thorax and neck where we thought it possible that the great lymphatic trunk might be, but our search was fruitless. We then examined the abdomen, first for the receptaculum chyle, and afterwards for mesenteric glands, again with negative results. Even upon microscopic examination the mesentery showed no trace of lymphatic glands (see fig. B). Finally, we were convinced that both lymphatic trunks and mesenteric glands were absent in this fœtus. The heart presented nothing peculiar in its condition, the foramen ovale was normal, as were the thyroid gland and other organs. There was no marked abnormality of the large blood-vessels of the thorax; this we remarked particularly, owing to the fact that abnormal thoracic ducts are frequently associated with anomalies of the large blood-vessels.

We had the mesentery, and the skin and subcutaneous tissue examined microscopically. In the mesentery no lymphatic glands nor traces of them could be detected; thus the result of our naked eye examination was confirmed. The sections of skin and subcutaneous tissue (see fig. D) presented a strange appearance, but still one that might be expected

where the lymphatic trunks were absent. Everywhere present in the sections were large spaces, in some parts empty and clear, in others filled with a colloid material, evidently coagulated lymph. From their appearance and position there was no doubt that these were enormously distended lymph-spaces, the over-distension being the result of the absence of the channels which usually draw away the contained lymph. In the normal process of circulation some of the liquor sanguinis exudes through the walls of the minute blood-vessels, passing in between the elements of the tissues, to supply them with the necessary nourishment, &c. From the interstices of the tissues this liquor or lymph is returned to the circulation by lymphatic vessels, which unite (are connected with glands in their course, as a rule), and finally form the large lymphatic trunks which open into the great veins. Now, if any link, or every link in the communication between the spaces of the tissues containing the lymph and the venous trunks be absent, there must result an accumulation of the fluid in the tissues, and as a consequence œdema. It is possible, it would appear, that the veins may *to a certain extent* take on the function of the lymphatics when they are occluded *in a limited region,* but when there is total absence of these channels throughout the body, then the veins cannot compensate for their absence. In the fœtus under consideration every portion of the connection between the lymph-spaces of the tissues and the venous trunk was absent, thoracic ducts, lymphatic glands and vessels; the exuded liquor saguinis possibly to a slight extent found its way back to the blood through the agency of the small veins; but if this were the case, the compensation was not sufficient, the exudation went on, the drainage of the spaces was deficient, the spaces became enormously distended, and the result was the aggravated condition of œdema already described. The case is so clear that we think it unnecessary to dilate upon the causation of the condition in this fœtus any further; the œdema was directly due to the absence of the various parts of the lymphatic system with the exception of the lymph-spaces. The cause of the non-development of these constituents of the absorbent system is a point which is extremely difficult of explanation, especially when our knowledge of the development of that system is at present so imperfect.

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EXPLANATION OF PLATE XXIII.

A. Portions of mesentery of normal fœtus, showing numerous mesenteric glands (natural size).

B. Portion of mesentery of œdematous fœtus, showing absence of mesenteric glands (natural size).

C. Head of œdematous fœtus, showing extraordinary appearance of parts produced by the œdema. No trace of an eye can be found on one side; it has been exposed by dissection upon the other (natural size).

D. Section of skin and superficial portion of subcutaneous tissue of œdematous fœtus, showing the enormously enlarged lymph-spaces, some of which are partly or completely filled with a colloid-looking material, apparently coagulated lymph (magnified).

CONTRIBUTIONS TO THE COMPARATIVE OSTEOLOGY OF ARCTIC AND SUB-ARCTIC WATER-BIRDS. PART IV. By R. W. SHUFELDT, M.D., C.M.Z.S.

(*Continued from page 427.*)

On the Osteology of the Auklets.—Some of the forms which we shall have to consider in the present part of this series of memoirs are, so far as their skeletons are concerned, the rarest of material to be found in any of our anatomical museums. Although I have not in my possession a number of the species of these diminutive Auks, yet I felt fortunate in securing skeletons of as many of them as I did, more especially of the exceptionally fine series of the representatives of the genus *Simorhynchus*. Our museums, in America at least, stand sadly in need of such material, and those who have enjoyed the opportunity of visiting the polar haunts of many of these birds were often too neglectful of such matters.

As already pointed out in Part I., the Auklets are contained in the genera *Cerorhinca*, *Ptychoramphus*, *Cyclorrhynchus*, and *Simorhynchus*, of the Subfamily PHALERINÆ, of the A.O.U. Check-list.

All of my efforts to secure a skeleton of *Cerorhinca monocerata* have already failed; while of *Ptychoramphus aleuticus* I have only an imperfect skull and legs of a specimen belonging to the Smithsonian Institution.

More especially I miss the first-mentioned type, as I am inclined to think that it will offer us in its osteology several interesting affinities with the *Fraterculinæ*.

No doubt a good series of skeletons of the Aleutian Auklet could also be studied with great advantage in the present connection; and, as far as I now know, some doubt exists in its case as to whether any of the parts of its bill are shed, as in those forms where it is known to take place.

It will be remembered that not so very long ago the ALCIDÆ were divided into two subfamilies (the *Phaleridinæ* and the

Alcinæ), and this latter fact had no little weight in the arrangement.

We must possess a far more exact knowledge of the morph-

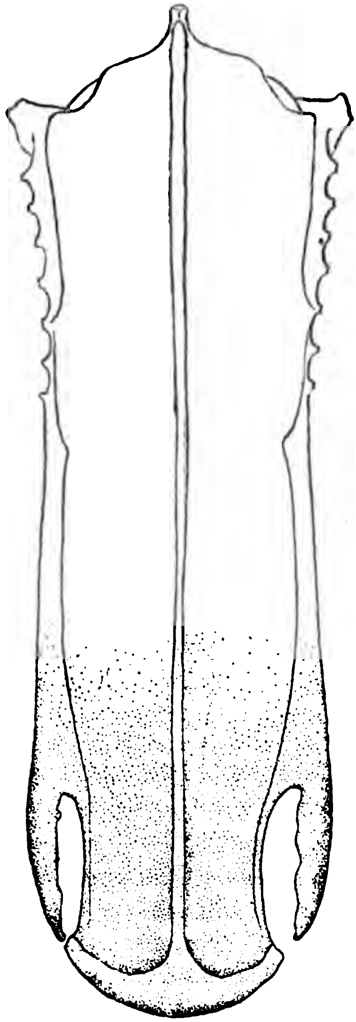


Fig. 1.—Outline of sternum of *Uria troile*, inferior aspect (specimen 3305, Smithsonian Collection); life size, by the author.

ology of the *Alcidæ* than we have at present before we can ever hope to obtain a clear idea of the probable affinities of the groups.

It is but too well known to me that my present efforts can be little more than a glimpse of that knowledge, and if they have but the effect of inducing others to collect a more extensive series of *alcoholics* of these birds, with the view of undertaking still more exhaustive researches to that end, it will be a great point gained.

As I have already stated upon more occasions than one, a study of the *Alcidæ* based upon the skeleton alone, although of great assistance, can never decide some of the exceedingly puzzling points in the affinities of the group; and I am confident that they never will be settled, if they are to be settled at all, without carefully digested studies of the other systems of their economy.

My material, given in the subjoined list, for a study of the osteology of the Auklets, comes entirely from the Smithsonian Institution; and I am indebted to Professor Baird for its use in the present connection.

Tabulated List of Material.

Specimens.	Where Collected.	Collector and Donor.	Catalogue No. of Smithsonian Institution Collection.	Remarks.
Ptychorhamphus aleuticus.	North-west coast.	John Gould.	11,178	Imperfect skull and pelvic limbs.
Simorhynchus pusillus.	North-west coast.	John Gould.	11,180	,, ,,
,, ,, ♂.	St Paul's Island, Alaska.	H. W. Elliott.	12,674	Skeleton. The majority of this series lack the skull, as skins were made from the specimens.
,, ,, ♀.	,,	,,	12,692	
,, ,, ♂.	,,	,,	12,673	
,, ,, ♂.	,,	,,	12,681	
,, ,, ♂.	,,	,,	12,679	,, ,,
,, ,, ♂.	,,	,,	12,707	,, ,,
,, ,, ♀.	,,	,,	12,699	,, ,,
,, ,, ♀.	,,	,,	12,687	,, ,,
,, ,, ♀.	,,	,,	12,669	,, ,,
,, ,, ♀.	,,	,,	12,667	,, ,,
,, ,, ♀.	,,	,,	12,666	Skeletons without skulls and parts of the limbs.
,, ,, ♂.	,,	,,	12,689	
,, ,, ♂.	,,	,,	12,708	
,, ,, ♀.	,,	,,	12,691	
,, ,, ♀.	,,	,,	12,676	
,, ,, ♀.	,,	,,	12,717	
,, ,,	,,	,,	12,712	
,, ,, ♀.	,,	,,	12,698	

List of Tabulated Material—continued.

Specimen.	Where Collected.	Collector and Donor.	Catalogue No. of Smithsonian Institution Collection.	Remarks.
Simorhynchus pusillus, ♀.	St Paul's Island, Alaska.	H. W. Elliott.	12,690	
,, ,, ♂.	,,	,,	12,710	
,, ,, ♂.	,,	,,	12,706	
,, ,, ♂.	,,	,,	12,698	
,, ,, ♀.	,,	,,	12,703	
,, ,, ♂.	,,	,,	12,678	
,, ,,	,,	,,	12,711	
,, ,, ♂.	,,	,,	12,686	
,, ,, ♀.	,,	,,	12,695	
,, ,, ♂.	,,	,,	12,680	
,, ,, ♂.	,,	,,	12,705	
,, ,, ♀.	,,	,,	12,670	
,, ,, ♂.	,,	,,	12,683	
,, ,, ♂.	,,	,,	12,604	Complete skeleton.
,, ,,	,,	,,	12,661	,, ,,
,, ,,	,,	,,	12,665	,, ,,
Simorhynchus cristatellus.	North-west coast.	John Gould.	11,176	Skull and pelvic limbs.
,, ,,	,,	,,	11,177	,, ,,
Simorhynchus psittaculus.	Alaska.	T. H. Bean.	3,465	Sternum.
Simorhynchus pusillus.	Behring Island.	Dr L. Stejneger.	17,012	Sternum, &c., ♀ æt. These valuable specimens were collected during December 1882 and January 1883.
,, ,, ♂.	,,	,,	17,013	
,, ,, ♂.	,,	,,	17,014	
,, ,, ♂.	,,	,,	17,015	
,, ,, ♀.	,,	,,	17,016	
,, ,, ♂.	,,	,,	17,017	
Simorhynchus pygmæus, ♀.	,,	,	17,018	,, ,,
,, ,, ♂.	,,	,,	17,019	,, ,,
,, ,,	,,	,,	17,020	,, ,,
,, ,, ♂.	,,	,,	17,021	,, ,,
,, ,, ♀.	,,	,,	17,022	,, ,,
,, ,, ♂.	,,	,,	17,023	,, ,,
,, ,, ♀.	,,	,,	17,024	,, ,,
,, ,, ♂.	,,	,,	17,025	,, ,,
,, ,, ♂.	,,	,,	17,026	,, ,,
,, ,, ♂.	,,	,,	17,027	,, ,,
Simorhynchus cristatellus, ♀.	,,	,,	17,028	,, ,,
,, ,, ♀.	,,	,,	17,029	,, ,,
,, ,,	...	...	12,964	Imperfect skeleton.

Before entering upon the osteology of *Simorhynchus pusillus*, which will be the form I shall choose to point out the skeletal characters of these Auklets, let us take a look at the imperfect

skull and pelvic limbs of the specimen of *Ptychorhamphus aleuticus*, and make a careful comparison of this skull (which includes the mandible) with *Cepphus grylle*, the Murrelets and *Simorhynchus*, as well as with the figure of the skull of *Alle* by Garrod.

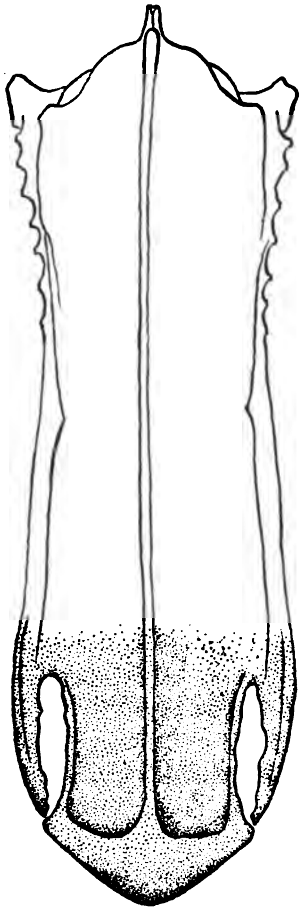


FIG. 2.—Outline of sternum of *Uria troile californica*, viewed from beneath (specimen 16,973, Smithsonian Collection); life size, by the author.

I must believe that it would be hard indeed to find a skull that could take with better grace an intermediate position in the series than this one. It seems to have in its structure the very mixture of characters of all these forms, as well as the

elaboration of others commenced by the Murres and Razor-bill. Its superior mandible is a veritable cross between *Brachyrhamphus* and *S. pusillus.* Its vomer has the anterior spine, and the maxillo-palatines agree exactly with *C. grylle.* The horizontal portions of the maxillary plates are not pierced by the circular foramen, and the hinder end of the palatines are truncate from behind forwards.

The superior surfaces of the lacrymals, which in *C. grylle* began to be elevated above the frontal region, are here arrived at to nearly the fullest extent to which that change is carried, it only being more highly developed in *S. psittaculus.* The roof of the orbit, which in the Murres and *Alca* reaches from the posterior border of one of these lacrymals to the anterior border of the peculiar wing-like post-frontal, is in this Aleutian Auk even more completely absorbed than it is in *C. grylle*, and the additional step has been taken on the part of the former in having the free edge of what now remains of the orbital vault nicely rounded off for its entire length.

The anterior wall of the brain-case is lacking over a large central area, including the foramina for exit of nerves. All osseous bulwarks between it and the orbits are absent. This leaves no foothold for the delicate lamina of the remains of the interorbital septum,[1] the posterior end of which now looks downwards in all the Auklets I have examined, as a free process, or more rarely to join the bone below.

The crotaphyte fossæ are lateral, and the vault of the skull smooth and globular. I can say nothing of the posterior aspect, as it has all been destroyed and cut away, the specimen no doubt originally being intended for a skin.

The symphysial extremity of the mandible is truncate from its lower posterior commencement forwards and upwards to the pointed apex. The surface is convexly rounded below, and longitudinally excavated above. Each ramus is nearly of equal width from the articular end to the posterior point where the symphysis begins rather deeper behind.

The borders are sharp above and rounded beneath, and the coronoid processes are but feebly developed.

[1] Figures of the skulls of these Auklets will be given in a Plate in the next Part.

The surangular is pierced by a foramen, but the true ramal vacuity is closed in by the splenial element. Sharp and recurved processes of as prominent a pattern as in any of the Gallinæ are seen to ornament each ramal angle.

The remains of the pelvic limbs which were saved with this mutilated skull lack the femora, and the leg-bones have been much crushed, particularly at their proximal ends. Enough remains, however, to convince me, by comparing them with the corresponding bones in other Auklets, that they closely resemble them; and, in the structure of the tarso-metatarsus, quite as nearly the Marbled Murrelet. The process anchylosed at the site of the accessory first metatarsal is fully as well developed as in the last-mentioned form.

On the Skeleton of Simorhynchus pusillus.

This diminutive sprite among the heavier water-fowl has a skeleton that, from its extreme delicacy, one feels more as if he were handling the skeleton of some of the medium-sized passerine birds, as that of Kingbirds, for example, rather than any of the feathered denizens of the ocean. Yet this fragile framework is indubitably stamped with all the characters of its kind.

The *skull* of *S. pusillus* presents all the features of the typical Auklets. The superior mandible is very broad transversely through the naso-maxillary articulations.

Viewed laterally, its apex presents a little tip that can hardly be termed a hook. Following the dentary border backwards from this point, it first presents a small concavity, then a gentle concavity to the maxillary.

The narial aperture is large, and shaped as in the Auk's generally, commensurable with the length of its beak.

The Least Auk is a schizorhinal bird like the rest of its kind, the nasals descending rather abruptly to their lower articulations. All the cranio-facial region between the lacrymals is concave, and these latter bones are raised above it as described above. A broad ethmoidal wing divides the orbit from the rhinal chamber, and above it a scroll of bone is developed that seems to be intended for the guidance and protection of the olfactory nerve as it passes over it. This, however, has nothing to do with another scroll-like or rather a spiral bone which

springs from the anterior surface of the ethmoidal wing of either side, its free end being anterior and in the rhinal space. Up to this point I have said nothing of this turbinal bone, although I have reason to believe that it may be present in all the Auks

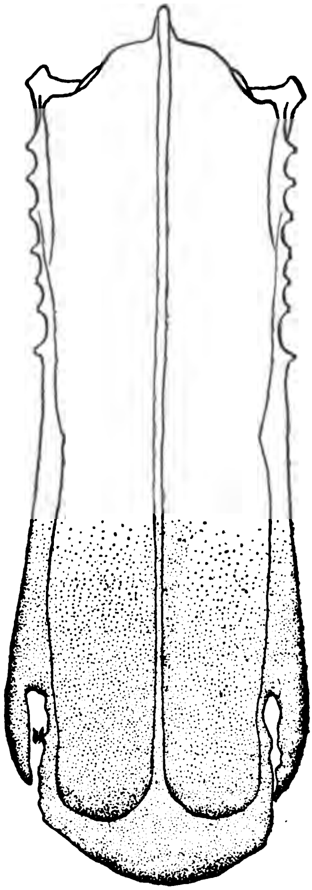


FIG. 3.—Outlines of sternum of Brünnich's Guillemot, viewed from beneath (specimen 16,783, Smithsonian Collection); life size, by the author.

and Guillemots described above. It is perfectly developed in this Least Auk, and in all the Puffins. During life the basal line of a ligamentous cone is attached to the anterior free edge of this bone and the conical semi-osseous, semi-ligamentous turbinal thus formed points forwards, and no doubt affords

abundant surface for the ramification of the terminal nerve-filaments of the olfactory. In Plate I. of Part V., which is to follow, I have represented this little turbinal bone in the rhinal chamber of *Fratercula corniculata*, and in the next figure on the same plate, in *Lunda cirrhata*, the same, with the soft parts attached and dotted. It does not appear in the skull of the Common Puffin, simply because it had been lost, and I could not draw what I did not see.

The ethmoid is pierced by a considerable foramen just anterior to its alæ, beyond which it is carried forwards for some distance in the median line beneath the premaxillary, to show the usual transverse slit in the region of the cranio-facial hinge.

Its anterior margin is sharp, and joins below the spike-like end of the rostrum that lies along the upper groove of the vomer.

The condition of the orbital septum and the antero-central wall of the brain-case agrees with the Aleutian Auk as described above. The peculiar wing-like post-frontals are as they exist in other Auklets, and shown in the figures. Very little change seems to take place in the quadrate bone among any of the *Alcidæ*. To all intents and purposes its form and facets remain pretty much the same, only varying slightly in shape throughout the group. *S. pusillus* has its crotaphyte fossæ confined to the sides of its skull, and but very feebly impressed, their upper boundaries being barely perceptible.

Regarding this skull from an upper view, we are at once attracted by the broad superior mandible, and the narrowness of the middle of the culmen. This, added to the narrow dentary processes of the premaxillary, allows a view between these parts, as I will show in my next Part in my drawing.

The frontal region between the orbits is reduced to a straight median bar of little width, and, not being connected to the inter-orbital system beneath, simply acts as a linking bridge between the antero-superior part of the brain-case and the lacrymo-frontal region. Posterior to its hinder abutment in the surface of the skull, the twin glandular depressions meeting in the median line are perceptibly stamped. To their rear the cranial vault has a smooth and rounded superficies.

Viewed from behind, this skull has a large but not a strikingly defined supraoccipital prominence.

The foramina which may pierce it on either side are some-

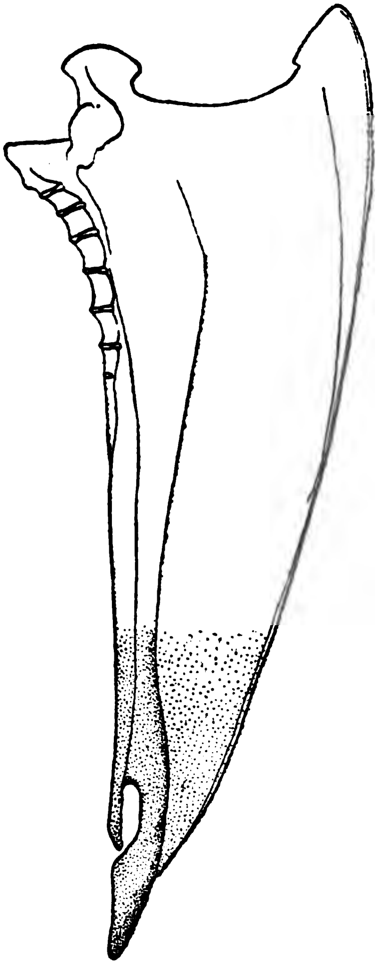


FIG. 4.—Outline of sternum of *Uria lomvia arra*; right lateral view (specimen 16,735, Smithsonian Collection); life size.

times so large as to expose the posterior peripheries of the semicircular canals of the middle ear.

The basal aspect of the skull of *S. pusillus* presents several points of interest. As we might expect, a large opening exists

between the dentary processes of the premaxillary that is of an elongated cordate outline with its base behind.

The maxillo-palatines are nearly flat plates of bone, not spongy, and quite in the horizontal plane. Their anterior edges and the solid part of the vomer all lie in the same transverse straight line, the anterior spine of the vomer alone projecting beyond. Mesially, the maxillo-palatines come quite close together, but the carination of the vomer and the inner edges of these bones form three parallel straight lines nearly the entire length of the former, their hinder ends being rounded in order to make room for the vomerine forks as they straddle the extremity of the rostrum and meet the ascending processes of the palatines.

These latter bones have their postero-external angles rounded, but in other respects their heads meet the heads of the slender pterygoids in a manner described above, and one which holds true for all the *Alcidæ*.

There is no evidence whatever of the presence of basi-pterygoid processes in the Auklet.

If the plane of the basi-temporal area were extended it would include, with but very slight departures, the occipital condyle, the mandibular facets of the quadrates, the pterygoids and the bones of the palate, and the dentary portions of the premaxillary. The maxillaries are not pierced by the single foramen in their horizontal plates.

The foramen magnum is cordate and large; it makes an angle of about 40 degrees with the basis cranii. The quadrato-jugal bar is straight and slender, and devoid of any projections between the quadrate and its anterior ending.

I fail to find an os uncinatum in these birds, and if they possess one it must be quite minute, and lost in all these specimens.

The *mandible*, except in point of size, agrees in all respects with that bone as found in *P. aleuticus*. The truncation of its symphysial end is more abrupt, however, and the symphysis shortened antero-posteriorly in consequence. Recurved processes are very prominent at the mandibular angles, rising far above the articular ends.

Sclerotal plates are present in the eyes of all Auks and

Guillemots, and now for the first time are here beginning to assume proportions incommensurate with other birds, attracting our attention to their larger size. This will receive especial

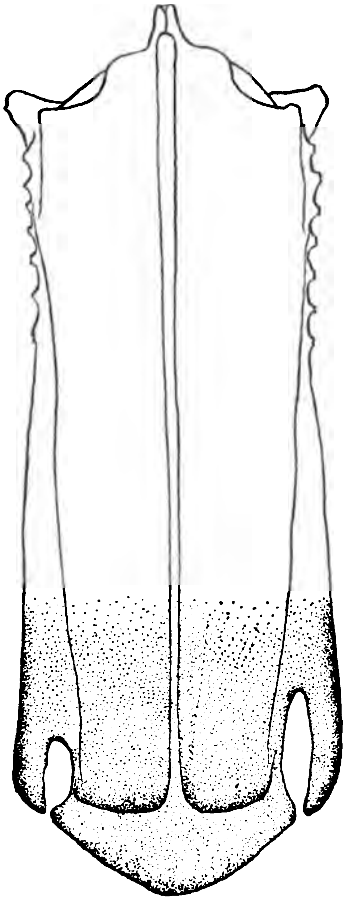


FIG. 5.—Outline of sternum of *Uria lomvia arra*, seen from beneath (specimen 16,735, Smithsonian Collection); life size.

investigation when we come to the Puffins, where they are very large and peculiarly shaped.

Figure 16 of Plate II. of the next Part (V.) gives the characters of the *hyoid arches* in a Puffin, and in all essential particulars they agree with our Least Auk, in which I have also

examined them. We are impressed by their extreme slenderness and delicacy in this little representative of the genus.

The long series of the incomplete skeletons collected by Mr Elliott permit me to present the characters of the cervical and dorsal regions of the vertebral column, the ribs, sternum, pectoral arch, and pelvis with probably an absolute certainty as they occur in this species, for I have carefully examined the entire collection. As the specimens were made into skins, of course they lack the skulls, limbs, and portions of the coccygeal vertebræ.

The *atlas* has a small hypapophysis which is bifid posteriorly. This process is well developed also on the axis, and still better on the third, fourth, and fifth vertebra, after that its place is usurped by the open carotid canal; this latter may be found in the sixth, seventh, and eighth as in specimen No. 12,661, or in the sixth, seventh, eighth, and ninth as in specimen No. 12,664, a hypapophysis occupying its place in the ninth vertebra in the first specimen. A neural spine is strongly developed in the axis, and gradually disappears down the series to be missing on the tenth vertebra. The lateral arterial canals are large, and the first pair of riblets occur free in the fourteenth vertebra throughout the series. A process (metapophysis) occurs on either side of the neural spine in the fifth to the tenth inclusive; in the eighth it is as conspicuous as the spine itself.

The fifteenth vertebra also supports a pair of ribs with free extremities, which bear unciform appendages.

In the dorsal region we find vertebræ with neural spines locking together at their upper angles, and further restricted in their motion upon each other by being laced with many bony spiculæ.

The hypapophysis occurs on the last four dorsals, while it is very long on the first one that precedes them, being shorter and tricornute on the fourteenth, fifteenth, and sixteenth. Eight more pairs of ribs occur posterior to the two free pair mentioned above. As a rule six of these connect with the sternum by hæmapophyses; the seventh may do so as an exception, but the last pair of all which articulate with the pelvis never do, nor do they bear as a rule epipleural appendages. These in the six pairs are wonderfully long and slender, being freely articulated with the posterior borders of the ribs to which they belong.

The form of these ribs agrees with the *Alcidæ*, generally being long and slender, sweeping posteriorly beneath the pelvis.

Little variation is exhibited on the part of the pelvis, its sacrum, or the vertebræ anchylosed between it and the iliac bones; these latter number thirteen, and are arranged much as they are in *B. marmoratus*, though the general form of the sacrum of the Least Auklet is more like *S. antiquus* than it is like the first mentioned bird.

The post- and pre-acetabular areas are about equal, and the ilio-neural canals are widely open. The double row of inter-apophysial foramina are constant on the dorsal aspect. Anteriorly, the ilia are truncate from before backwards, while their internal and external borders are concave outwards, as well as parallel to each other. This determines their form from the acetabulæ to their anterior ends, over which space their superficies are gently and uniformly concave and smooth.

Foraminal openings on the lateral aspect of the pelvis agree with the *Alcinæ*, but the strait connecting the obturator foramen and space is here very narrow again. Post-pubic elements are still long, and there is no evidence of a pro-pubis. The notch between the ilium and ischium on the posterior border is shallow.

S. pusillus has nine vertebræ in its tail and a pygostyle. They all bear a close resemblance to these bones, as we found them in *C. grylle*.

The last five or six have small free chevron bones, that are notched at their anterior ends.

This Auklet has a *sternum* that (although it is characterised as the bone is among the group generally, so much so that a glance is sufficient to satisfy us that it belongs to an Auk) exhibits a pattern peculiarly its own (compare the figures of sternum in this and preceding Parts). This is due principally to the form assumed by the xiphoidal extremity. As a rule, six facets are found upon each costal border; there may be seven as an exception.

The manubrium has sunk backwards between the coracoidal beds; it is without keel, and much aborted as compared with the process in some of the *Alcinæ*. The sternum is much thickened about it, and in the internal aspect behind it and

between the costal processes a flat triangular, nearly vertical, wall occurs—the anterior wall of the body. The carina has the form of this part in common with other Auks, but its posterior ending is much farther removed from the extremity of the sternal body. The muscular line on either side runs down from the base of the costal process to this posterior carinal insertion. A large foramen is found between it and the external border on either side, and a notch may occur in the middle.

The sternum is narrow transversely in its fore part, and gently and generally swelled out behind. It is much more concave on the thoracic aspect than in the Murres, for instance, where it is nearly flat.

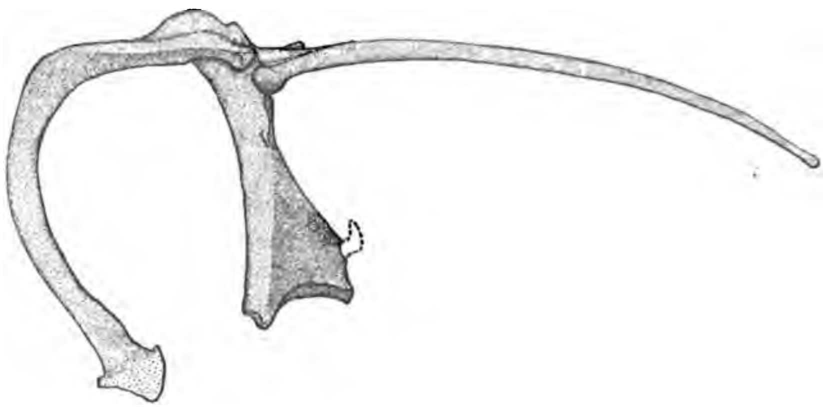


FIG. 6.—Inner aspect of right half of shoulder girdle of *Uria lomvia arra* (specimen 16,735, Smithsonian Collection); life size.

When comparisons come to be made further on with others of the subfamily, I will have additional observations to make upon this bone.

In the pectoral arch the construction of the heads of the clavicles is upon the same plan as described for the Murrelets. Their length is comparatively much less, and would not particularly attract our attention.

Below, the furculum is rather delicately fashioned; the U is deep, and the hypocleidium small. On the coracoid the scapular process is never pierced by the foramen, as described for *Alca* and others; indeed, it does not descend far enough on its shaft to admit of it.

The process low down on the external border of the shaft of the bone is also done away with to a very large extent. Each scapular blade is long and narrow, tapering to a rounded point behind, but is not truncate. Its head is wide transversely, but much compressed from above downwards. It is closely approached by the furculum, but the tip of that bone touches neither this nor the scapular process of the coracoid.

The entire arch is non-pneumatic.

Except the flattening of the bones of the brachium and antebrachium, the pectoral limb of the Least Auk present all the characters I have ascribed to it in the other members of the group, omitting *Alca*, and perhaps some few points in *Uria*. In the humerus we note that the radial crest is rather better defined, though still a low ridge, but ends abruptly on the shaft distally, and does not gradually merge into it, as in such forms as the Black-throated Guillemot and others. Its head, or the articular part of it, curls over in the anconal direction to a striking degree. Ulnar crest is prominent, and the pseudo-pneumatic foramen deep, though not only this bone, but, as in other Auks, the entire pectoral limb is non-pneumatic. The shaft is sub-cylindrical, and a small ectó-condyloid tubercle is present.

Its distal extremity is constructed much as it is in the Murrelets.

The shafts of both radius and ulna are, comparatively speaking, rather stouter than in the other Auks. On its sharpened border the former bone is marked by a distinct row of papillæ for the quill-butts of the secondaries. They are pitted at their apices.

All three sesamoids, found in many of these birds about the elbow, are present in the Least Auk, occupying the same positions as in the Puffins.

The one marked *ss''* in fig. 47, I propose, for convenience sake, to call the *ulnar sesamoid*. It is fully developed in the present species, as is the olecranon which overshadows it.

In its general character the skeleton of manus in this little Auk is not at all unlike the one in the figure I have first referred to. It agrees with it in having the little claw (which in neither form pierces the integuments), and in retaining the three pro-

cesses I have described for other Auks. These are—one on the front of the shaft at its lower end, both in carpo-metacarpus and the proximal expanded phalanx of index digit, and the third one at the opposite lower angle of the latter bone. In the Puffin, however, these first two processes are much rounded off and quite near gone, so as to hardly attract our attention.

S. pusillus has a humerus which is 3·5 centimetres long; an ulna 2·9; radius, 2·7; carpo-metacarpus, 1·9; pollex phalanx, 0·6; proximal phalanx of index, 0·9; its distal one, 1·1; and the middle finger's phalanx, 0·5 centimetres long. All the bones of the pelvic extremity of the Least Auk are non-pneumatic, but with medullary cavities of considerable size.

The trochanterian ridge of the femur does not rise above the summit of the bone; the shaft is sub-cylindrical and straight.

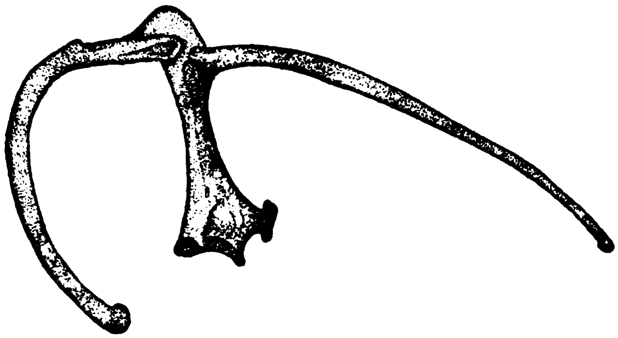


FIG. 7.—Inner aspect of right half of shoulder girdle of *Cepphus columba* (specimen 3294, Smithsonian Collection); life size.

Of the two condyles the outer is the lower and most posterior. A small patella exists, surmounting the cnemial crest of tibia as in *Uria* and others.

The head of tibia, including the cnemial ridges, is slightly bent to the outer side. These ridges are constructed like in the *Alcinæ*, varying but slightly in form.

The tibial shaft is straight, and the tendinal groove below is bridged over by the osseous bar for tendinal confinement. Below its ridge, on the side of the tibial shaft, the fibula is unusually small; it anchyloses with the large leg-bone at its lower part, about half-way down.

The hypotarsus of the tarso-metatarsus is both perforated

and grooved for the passage of the flexor tendons, and it is comparatively more prominent than in the *Alcinæ*.

Otherwise this segment of the pelvic limb does not depart to any marked degree from the bone as it is seen, for instance, in the Marbled Guillemot, the principal differences being that in the Least Auk the bone is more slender; the hypotarsus differs as stated above, and the process at the site of the accessory metatarsal is not present.

The phalanges resemble these bones as seen in the Murrelets. Measurements of the bones of this limb show the femur to be 2·2 centimetres long; the tibia, 4·0; the fibula, 2·4; the tarso-metatarsus, 2·0; proximal joint of outside toe, 0·65; next, 0·5; next, 0·51; next, 0·55; and the claw, 0·37; middle toe, proximal joint, 0·9; next, 0·61; next, 0·58; and its claw, 0·5; and the inside toe, proximal joint, 0·8; next, 0·6; and its claw, 0·4.

This sketch of the skeleton of *S. pusillus*, taken in connection with all that has been said before about the osteology of the *Alcinæ*, I trust will prove sufficient to place before the reader a clear picture of this part of the anatomy of an Auklet. In its delicate little skeleton we find all those characters which the strongly-marked genus of *Simorhynchus* has to distinguish it. So much so, that in fact my labour will be much lightened in treating the other forms contained in it, for despite the extraordinary ornaments assumed by some during the breeding season, we will find that structurally these birds are evidently of very close relationship.

Remarks upon the Skeleton of Simorhynchus cristatellus.

In their seasonal plumages these two little Auks, *S. pusillus* and the present one, certainly look very unlike each other, yet notwithstanding this I doubt very much that the skeletons of any two birds of different species could be found that were fundamentally more alike.

Nowhere does this apply with more truth than it does to the skulls of these birds. It would be hard to find, indeed, a good distinguishing character between them beyond their difference in size. So when I have said,—skull, including mandible, of *Simorhynchus cristatellus*, like that of *S. pusillus*,—I feel that

I have done my full duty, especially after the pains taken to clearly define, as I hope I have, the character of this part of the skeleton of the latter form.

The skull of the Crested Auklet is nearly double the size of the Least Auk, or fully more than one-third larger; it is rather more so back, and shorter for its width also, than in the former species.

The vertebral column and ribs agree in both birds, and the same may be said of the pelvis and pectoral arch.

One important change has come about in the vertebræ of the dorsal region in all the members of this genus so far as my material will permit me to say,—and this is, that the opisthocœlian method of articulation between the centre of these vertebræ is not apparently characteristic of them. They articulate very much as do the bones in the cervical region, with perhaps their heterocœlian nature not quite as strongly marked.

The valuable series of sterna brought back by Dr Stejneger from Behring Island in 1883 enable me to make some comparisons and remarks upon this bone, as referring to the form it assumes in the genus as a whole. Among these sterna will be noticed the large assortment of that rare little Auk, *S. pygmæus*, and I am only sorry that that indefatigable explorer of those islands did not think to add a few complete skeletons of this bird to his collection when the opportunity seemed to be such a good one.

I have drawn outline figures, which illustrate this memoir, of the pectoral aspects of characteristic specimens of this series, and the reader's attention is invited to them, as offering a better idea of the form of the sternum in *Simorhynchus* than perhaps anything I might be enabled to write about them (see figs. Plates III. and IV., Part V.).

Their general character upon this view is expressed by saying that they are narrow in front, with six facets on each costal border; nearly aborted manubrial process; and that the angle of the carina does not pass in front of a plane erected perpendicular to the most anterior part of the sternal body. Behind, the body of the bone is convex on this surface, and, notwithstanding slight variations that may exist, the fundamental plan is, that this part is swelled out, the xiphoidal extremity more

or less produced beyond the hinder ending of the carina, rounded, and exhibiting a large oval foramen on either side, wide in some cases, narrow in others, but the long axis of which, if produced, would intersect either at the posterior xiphoidal margin in the median line, or a short distance beyond it behind.

Through a lack of complete ossification sometimes, the outer peripheries of these foramina are cut through the body of the bone to the posterior margin, but in no instance is the sternum of a typical *Simorhynchus* notched.

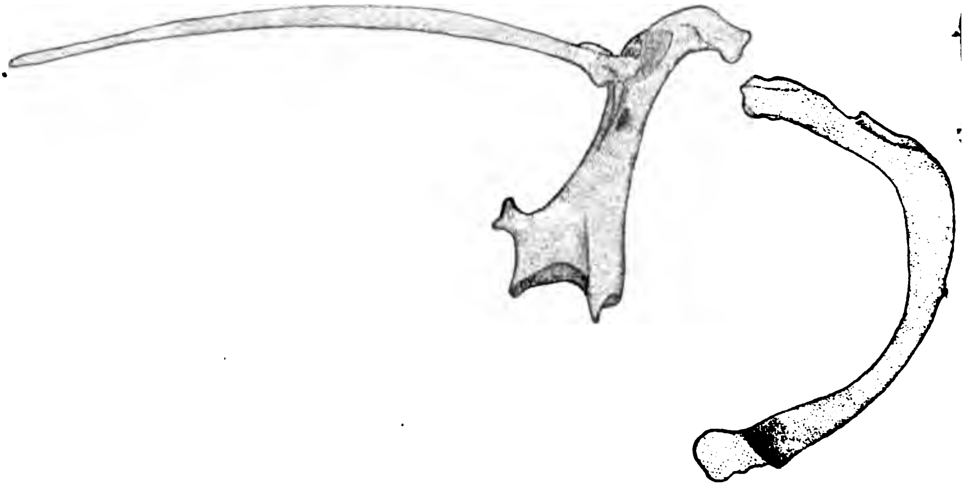


FIG. 8.—Inner aspect of left half of shoulder girdle of *Uria troile* (specimen 3305, Smithsonian Collection). The furcula detached; life size, from the specimen.

As in the figure of *S. cristatellus*, a few small irregular vacuities may occur, but these are due to the bone not having been thoroughly ossified, and have nothing to do whatever with the formation proper of the sternum.

They may even occur in the anterior part of the bone, as shown in the specimen No. 17,028, and figured in the series.

I would remark here that in the series of sterna of *S. pygmæus* considerable variation is seen in the form of these xiphoidal foramina, the width and length of this extremity and its own outline depending upon the extent of ossification it has enjoyed. All these conform to make these bones look quite unlike and of different lengths; but on the whole the general plan is the

same, and, assisted by the difference in size, easily distinguishable from others of the genus.

When these birds have their pectoral arches articulated, as in life, we find that the shaft of the coracoid is in the same straight line with the costal border; and further, that the rather slender and broad U-shaped furcula curves backwards, so that its small hypocleidium is seen to be just above the superior margin of the prominent carinal angle.

It is hardly necessary to add that *S. cristatellus* has precisely the same form to the skeleton of its thoracic parieties as seen in other Auklets, though among these birds the ribs do not sweep back quite as far comparatively as they do in the Murres and the Razor-bill.

Remarks upon the Osteology of the Genus Cyclorrhynchus.
(C. psittaculus.)

In many respects the Paroquet Auklet bears the same relation to the genus *Simorhynchus* that the Razor-bill Auk does to the genus *Uria.* My comparison applies more particularly to the form of the osseous mandibles of the types thus compared. Very little difference is to be found between the hinder half of the skull of *Alca torda* and the corresponding part in a skull of the Murre, but just about as much as we find upon comparison of the hinder halves of the skulls of *Cyclorrhynchus* and *S. cristatellus;* yet the forms of the osseous mandibles of these last two genera are quite unlike.

This will be well shown for the lateral view in figures in Plate II. of the Part which will follow the present one.

Simorhynchus pusillus, then, exhibits the form of the superior osseous mandible that is common in the greatest number of its kind at present known to us. The manner in which this differs in the subject in hand is easily seen in the side view of its skull. Although the amount of lateral compression of this part in the Paroquet Auk does not approach what we find in the Razor-bill, still the convex prominence of the anterior half of the culmen is very much the same.

It is quite evident, however, that these two birds have the lower margins of the superior mandibles and their apices entirely

different, being doubly curved in *Alca* and convex downwards for its entire length in *C. psittaculus.*

In one of the specimens of this latter Auklet the interorbital septum is better ossified than I have said elsewhere is the rule for it to be.

The optic foramen and the smaller one to its outer side are both nearly intact, the first simply having a small break in its periphery on either side that communicates with the general opening of the anterior wall of the brain case.

The symphysial part of the mandible in the Paroquet Auklet is turned upwards in a sharpened point, in order to accommodate its form to that of the other part of the bill above.

Further than this, I find nothing in the entire skull and mandible of this bird that differs sufficiently with others of the genus to be worthy of special mention and record.

I consider the differences mentioned, taken in connection with the external characteristics of this bird, as very excellent specific ones, but in no way entitled to any higher grade.

The hyoid arches are constructed upon the same principle as those in the other Auks described above; the cerrato-hyals sometimes ossify very feebly, and it would not surprise me to find them in some specimens built entirely of cartilage.

The process at the site of the accessory metatarsal, anchylosed to the shaft of the tarso-metatarsal, is prominent in *C. psittaculus*, with this exception, and the fact that the skeleton is less than half as large again as the skeleton of *S. pusillus*, its remainder agrees, in many instances even to minor details, with the skeleton of that Auklet.

In both birds a minute sesamoid may be found at the proximal ends of the phalanges of the toes in the flexor tendons; the most constant one being found in connection with these parts is that of the proximal phalanx of the inner toe.

In the next Part, or Part V., we will take up the skeleton in the Puffins or the subfamily *Fraterculinæ.*

ON THE DEVELOPMENT OF THE TASTE-ORGANS OF MAN. By FREDERICK TUCKERMAN, M.D., *Amherst, Massachusetts.*

WHILE it will not be denied that something has been accomplished of late years towards a better understanding of the nature and distribution of the mammalian taste-organs, as well as a clearer recognition of their behaviour when exposed to different and often widely varying conditions, yet it must be conceded that, so far as their mode of development is concerned, our knowledge is still very limited. The valuable researches of Drasch[1] and of Hermann[2] on the more intimate structure of the gustatory papillæ and taste-bulbs (notwithstanding a failure on the part of these observers to agree in many of their conclusions), not only throw light upon several important questions which had hitherto been veiled in almost complete obscurity, but they also reveal new fields of inquiry for the conscientious investigator. To the labours of these histologists should be added those of Griffini.[3] This observer approached the subject mainly from the experimental side, and studied the taste-organs with a view to learning, if possible, something of the phenomena of reproduction and regeneration. Of the important results obtained by him I shall have occasion to speak a little later in the course of this paper.

HISTORICAL REVIEW.

Hans v. Wyss[4] is the earliest writer on the taste-organs who, so far as I am aware, makes any allusion to their appearance at different

[1] "Histologische und Physiologische Studien über das Geschmacksorgan," *Sitzb. d. k. Akad. d. Wiss. Wien*, Bd. lxxxviii. Abth. iii. p. 516, 1883; "Untersuchungen über die Papillæ foliatæ et circumvallatæ des Kaninchen und Feldhasen," *Abhandl. d. k. s. Gesellsch. d. Wiss. Leipzig*, Bd. xxiv. p. 231, 1887.

[2] "Studien über den feineren Bau des Geschmacksorganes," *Sitzb. d. math.-phys. Classe d. k. b. Akad. d. Wiss. München*, p. 277, 1888.

[3] "Sulla riproduzione degli Organi Gustatorii," *Rendiconti Reale Istituto Lombardo*, ser. ii. vol. xx. p. 667, 1887.

[4] "Die becherförmigen Organe der Zunge," *Arch. f. mikr. Anat.*, Bd. vi. p. 237, 1870.

stages of growth. He examined the papilla foliata of new-born and partly-grown rabbits. In the new-born rabbit he found the foliate organ quite perfectly formed, and experienced no difficulty in identifying taste-bulbs. The bulbs of this period, however, differed from those of the full-grown animal in having a more rounded shape, and in being less than one-half as large. Within three weeks this difference ceased to be longer noticeable.

J. Hönigschmied,[1] in a communication on the microscopic anatomy of the taste-organs, merely states that he failed to detect in the circumvallate papillæ of the new-born child any regular arrangement of the taste-bulbs.

Hönigschmied was followed a little later by Hoffmann,[2] who investigated the human embryo and new-born child for the purpose of studying the distribution of the taste-organs in man. The earliest organs examined by him came from an embryo three and one-half months' old, and the oldest from a woman about sixty years of age. In a fungiform papilla of a four and one-half months' fœtus, and also in the papillæ of one at the sixth month, taste-bulbs were present. In the six months' fœtus the peripheral ends of the supporting cells of the bulbs were prolonged to an unusual extent, giving the bulbs somewhat the form of a matrass. Hoffmann concludes that taste-bulbs are more frequent in embryos and the newly-born than in older individuals; that in embryos and new-born children they occur more frequently and in greater number on the free surface of the papillæ than in the adult, and that in old persons they are but rarely met with in this region.

In 1884, both Hermann[3] and Lustig[4] published papers on the development of the taste-organs in mammals. The former investigator confined himself wholly to an examination of the circumvallate and foliate papillæ of the fœtal and new-born rabbit, whilst the latter studied these organs in both the rabbit and man. Hermann and Lustig were the first histologists to make a special study of the evolution of the taste-organs of the rabbit, whilst to Lustig is due the merit of first investigating, in detail, the development of the taste-organs of man.

According to Hermann, the development of the gustatory papillæ takes place during the latter period of intrauterine life and in the first few days following birth. In a rabbit embryo, 54 mm. long, he was able to distinguish, with the unaided eye, the circumvallate and foliate papillæ, but the trenches of the former and furrows of the latter were wanting. With reference to the development of these

[1] "Ein Beitrag zur mikroskopischen Anatomie der Geschmacksorgane," *Zeitsch. f. Wiss. Zool.*, Bd. xxiii. p. 414, 1873.

[2] "Ueber die Verbreitung der Geschmacksknospen beim Menschen," *Virchow's Archiv*, Bd. lxii. p. 516, 1875.

[3] "Beitrag zur Entwicklungsgeschichte des Geschmacksorgans beim Kaninchen," *Arch. f. mikr. Anat.*, Bd. xxiv. p. 216, 1884.

[4] "Beiträge zur Kenntniss der Entwickelung der Geschmacksknospen," *Sitzb. d. k. Akad. d. Wiss. Wien*, Bd. lxxxix. Abth. iii. p. 308, 1884.

papillæ, Hermann (*loc. cit.*, p. 227) makes the following statement:—"Fasst man nun die Resultate vorliegender Untersuchung zusammen, so ergibt sich für's erste, das die Papilla foliata und vallata aus einfachen Epitheleinstülpungen sich entwickeln, welche dadurch, dass sie seitliche Fortsätze—secundäre Epitheleinstülpungen—treiben, bei ersterer zur Bildung der secundären Blätter, bei der Papilla vallata des Walles Anlass gaben. Die primären Epitheleinstülpungen sind bei Kaninchenföten von 50 mm Länge, also vom 23. Tage, schon vorhanden, die Bildung der secundären Blätter, resp. des Walles, beginnt jedoch erst bei föten von 70 mm Länge, nach dem 24. Tage des intrauterinen Lebens und ist bei Neugeborenen noch nicht zum Abschluss gekommen." The complete differentiation of the circumvallate papillæ and of the folds of the foliate organs ensues only after birth. Respecting the mode of formation of the serous glands, Hermann says:—"Ausser zur Bildung der Papillen stehen die primären Epitheleinstülpungen noch in Beziehung zur Genese der an die Geschmacksorgane eng gebundenen Ebner'schen acinösen Drüsen, indem sie als anfangs solide Zellstränge in das Muskelgewebe hineinwuchern, durch Atrophie der central gelegenen Zellen sich zu blind und kolbig endenden Gängen aushöhlen, von denen sich seitliche Ausbuchtungen—die Acini—abzweigen. Dieser letztere Process findet ebenfalls erst beim neugeborenen Kaninchen statt."

In a rabbit's embryo, some 50 mm. in length, Hermann found taste-bulbs, in the first stages of formation, on the free surface of the circumvallate papillæ. In an embryo rabbit, 70 mm. long, the bulbs of this area were perfectly developed and numerous. In the secondary lamellæ of the foliate organ and lateral wall of the circumvallate papillæ of an embryo, 95 mm. long, were seen the forerunners of the definite taste-bulbs, in the form of modified basal cells of the epithelium. In embryos of a later period these fusiform cells traverse the entire thickness of the epithelial investment of the papilla. At birth a few of these bulbs had matured, and by the sixth day of life their development was completed. With the appearance of the definite bulbs those of the free surface (having attained their completion during intrauterine life) undergo degeneration, and by the third day there is scarcely a vestige of them remaining.

Lustig failed to discover taste-bulbs in rabbit embryos; even in those 10 cm. in length the papillæ were destitute of them. He therefore inferred that taste-bulbs are utterly lacking in the embryonic circumvallate and foliate papillæ. The smallest rabbit embryos investigated by him were from 6 to 7½ cm. in length. In these the circumvallate papillæ were sufficiently advanced to be recognised with the naked eye; the foliate organs, however, required the microscope to reveal their presence. In a rabbit 12 cm. long, and which had lived thirty-six hours, the circumvallate and foliate papillæ bore taste-bulbs in various stages of development. Those in the incipient stages of growth consisted of three to six strongly refractive taste-cells, the peripheral extremities of which protruded through the taste-pore. Lying between these cells were broad, swollen, nucleated, spindle-shaped ones, which Lustig considered the future supporting

cells. The development of the bulbs of both gustatory areas was not fully completed until the beginning of the third week following birth.

The youngest human tongue investigated by Lustig came from a fœtus of the fifth month of intrauterine life. Seated near the base of this tongue were five circumvallate papillæ. The foliate organs also were visible. No taste-bulbs were detected in either taste-area or elsewhere on the tongue. The next tongue examined came from a fœtus of the seventh month, and possessed seven circumvallate papillæ. These papillæ differed from those just mentioned in having their lateral area entirely protected by the enclosing wall; in the former, the outer wall only protecting the papillæ in their lower third. Some of these papillæ bore on their free surface facing the buccal cavity small, but sharply-defined, and, in some cases, well-developed taste-bulbs. The bulbs of the foliate papillæ were less numerous, and only present on the exposed surface of the folds, the furrows being filled for more than half their depth with epithelium. In the circumvallate papillæ of a child born at the beginning of the eighth lunar month, the bulbs still exhibited the embryonic characters. The foliate areas of this child were well formed, and possessed bulbs on both the free surface and upon the sides of the folds. In a mature still-born child, all of the circumvallate papillæ bore bulbs, yet not in all cases on their lateral wall. On one of these papillæ was superposed a papilla of the fungiform type, bearing bulbs on both its lateral slopes. In a normally developed child, which died twelve hours after delivery, all of the circumvallate papillæ contained bulbs, but they differed in size, form, and arrangement from those of the adult.

Griffini's[1] recent researches on the reproduction of the gustatory papillæ and regeneration of the taste-bulbs in the rabbit and dog are of signal value. From his experiments it appears that after excision of a foliate papilla of the rabbit, the area corresponding to the part removed is shortly revested with pavement epithelium. Later, from the sixteenth to the twentieth day a few small hemispherical elevations make their appearance, and these subsequently increase in size and number. During this period also many of the injured gland-ducts undergo repair, and communicate with the free surface of the epithelium. Within the secondary papillary processes of the elevations above referred to, taste-bulbs, lying partly in the mucosa (and in process of formation), first make their appearance. Thirty days after the complete removal of the circumvallate papilla of the dog a newly-formed papilla makes its appearance, having, however, the characters of the fungiform type. At the fortieth day (in a single instance only) a few taste-bulbs, situated at the lateral margin of the new papilla, were seen. Following section of the glosso-pharyngeals, the papillæ are changed but slightly, but the taste-bulbs begin to degenerate within twenty-three hours. The taste-cells are first destroyed, disappearing completely by the fifth day; the supporting cells soon after undergo

[1] *Op. cit.*

atrophy, and by the twenty-eighth day no bulbs are visible. At the seventy-sixth day after the division of the nerves, bulbs in various stages of formation were seen; but by the 209th day their development was still incomplete. According to Griffini, reproduction of the taste-bulbs, following the removal of a papilla or after section of the glosso-pharyngeal nerve, is effected in the following way:—The axis cylinders of the divided nucleated nerve-fibres are regenerated and penetrate the epithelium; active proliferation of the adjacent epithelial cells then occurs, the latter placing themselves around the intra-epithelial nerve-fibrils, and forming the supporting cells of the bulbs.

In comparing some of the results arrived at by the foregoing observers, we notice first a want of harmony in the expressions of v. Wyss and Hermann respecting the appearance of the foliate organ in the new-born rabbit. The former says [1] that this organ is quite perfectly formed in the new-born rabbit, and that bulbs can be detected without difficulty, the latter differing in size and form only from those of the adult animal. Hermann, on the other hand, maintains [2] that genuine epithelial bulbs, as seen in the full-grown animal, are found only very isolated in the newly-born rabbit, and are more fusiform than those of the adult. According to Hermann, the foliate organ does not acquire its definite form until the sixth day of life, and even then the bulbs are different in their structure and arrangement from those of the full-grown rabbit.

The statements of Hermann and Lustig are likewise not entirely in accord. While the former recognised taste-bulbs, in an early stage of formation, on the free area of a foliate papilla in a rabbit embryo 54 mm. long, and found them numerous and comparatively well advanced in the same region of a circumvallate papilla of a rabbit embryo 70 mm. in length, the latter [3] failed to discover them in rabbit embryos at all, and, in consequence, was led to doubt their existence during intrauterine life.

Hoffmann [4] found embryonic taste-bulbs in a fungiform papilla of a four and one-half months' fœtus, and in the papillæ of one at the sixth month. Lustig failed to detect bulbs in the papillæ of a fœtus at the end of the fifth month,[5] but in one at the seventh he found on the free upper surface of both circumvallate and foliate papillæ small but well-defined bulbs.

The views of most of the investigators which I have cited are somewhat at variance respecting the nature of the taste-bulbs and their mode of origin, but I will not prolong this paper by discussing them.

Present Investigation.

I am greatly indebted to Dr William F. Whitney, curator of the Anatomical Museum of the Harvard Medical School, and to

[1] *Loc. cit.*, p. 254. [2] *Loc. cit.*, p. 221 *et seq.*
[3] *Loc. cit.*, pp. 311, 315. [4] *Loc. cit.*, pp. 526, 529.
[5] *Loc. cit.*, p. 317.

Dr John G. Stanton, of New London, Conn., both of whom very kindly placed at my disposal much of the material used in this research.

The youngest tongue which came under my observation was taken from a fœtus at about the end of the fourth month.

Microscopic Appearance.—The upper surface of the tongue is marked by a wide, and in places deep, longitudinal mesial groove running nearly the whole length of the organ. The posterior dorsal surface is covered with papillary elevations of the mucous membrane, which present a great diversity in size and shape. The corresponding surface of the fore part of the dorsum is comparatively smooth and level. Near the lateral contour of the tongue proliferation of the epithelium appears to be most active. Here and elsewhere the epithelial cells may be seen pushing into the mucosa, some of their nuclei showing indications of karyokinetic figures. The cells composing the outer layers of the stratified pavement epithelium are large and chiefly cuboidal or polyhedral in form. The epithelium covering the papillary elevations does not differ greatly, save in the size of the cells, from that investing the lingual papillæ of later fœtuses. The superficial layer, which is more or less thin, is formed of ordinary pavement epithelium.

Internal to this layer is a much thicker one, consisting for the most part of spheroidal cells with prominent nuclei, and below this again is a deep layer, composed entirely of elongated but not true columnar cells, which are in contact with the mucosa. Quite frequently the middle and deep layers are so thoroughly blended as to obliterate completely the line of demarcation between them. The connective tissue of the mucosa and submucosa is rich in nuclei and delicate fibrils. The stroma of the submucosa is somewhat looser in texture than that of the mucosa, and at various points where the epithelium has penetrated it to a considerable depth changes are perceptible, which suggest the incipient stages of development of the serous glands and their ducts. The transverse striæ of the muscle-fibres of this tongue require a comparatively high power to resolve them.

On the posterior dorsal surface, near the base of the organ, are five papillæ of the circumvallate type. The largest and most advanced of these papillæ is situated directly in the median

line of the tongue, and measures 0·13 mm. transversely and 0·15 mm. in height. The papillæ comprising this type project but slightly from the surface. Two adjoining ones show a decided tendency to share an enclosing wall in common. Fungiform papillæ, in various stages of growth, are scattered over the posterior dorsal region, and the foliate organs, in a formative stage, are clearly recognisable in the irregular elevations of the mucosa at the sides of the base of the tongue. The upper surface of the circumvallate papillæ is flattened or slightly convex, and the sides are perpendicular, or inclined slightly inwards. The trenches are not yet differentiated, although their future position is, in most instances, clearly delineated. The mucosa filling the interior of the circumvallate papillæ is perfectly homogeneous in appearance, and does not differ in character structurally from that underlying them.

In one of the smaller circumvallate papillæ is a taste-bulb in an early stage of development. It lies vertically directly in the long axis of the papilla. Its component cells, which are separable with a high power, converge peripherally and form an apex, which penetrates the outer layers of epithelium. The base of the bulb is completely lost in the mucosa. Four sensory cells are distinguishable, each of which possesses a relatively large oval nucleus, situated in the lower half of the cell. This embryonic terminal organ measures 0·0165 mm. in length and 0·012 mm. in breadth. Here and there, in the epithelium and connective tissue of these papillæ, modifications of the cells and stroma were unmistakable, but the precise nature of these changes I was unable to determine, nor could I in all cases establish with certainty the identity of the elements themselves.

The next tongue which I examined came from a fœtus four and one-half months' old, and, like the preceding, required the microscope to reveal its superficial structures.

Microscopic Appearance.—The dorsal surface of this tongue is more markedly papillose than that just described, and at its extreme posterior portion the mucous membrane is thrown into a number of irregular folds. The epithelium covering the circumvallate papillæ does not differ greatly in arrangement from that of the new-born child. The epithelium, however,

overlying the general lingual surface is relatively much thicker than in newly-born children. The external layer of stratified pavement epithelium is very thick, and fills up to a common level most of the depressions and interstices between the various papillæ. The middle epithelial layer, as a distinct layer, has in places almost ceased to exist, and the deep or internal layer is composed of true columnar cells. The mucosa and submucosa are quite readily distinguished one from the other, and in the stroma of the latter the glands have advanced to some degree, and here and there are beginning to take definite shape.

At the posterior part of the dorsum of this tongue are six circumvallate papillæ, one or two of which are undergoing transition from the fungiform type. Some of these papillæ show indications of lobation. The trenches are still filled to the level of the free surface with pavement epithelium, and that protecting the upper exposed area of the papillæ is continuous with the adjoining lingual epithelium. The epithelium of the upper surface has increased in thickness without a proportionate increase in the thickness of that investing the lateral area. The papillæ vary in size, but one of average dimensions measured 0·35 mm. in its transverse diameter and was 0·20 mm. in height. The foliate organs consist of a few folds of the mucous membrane, the spaces between which are filled up to one level with epithelium.

The greater number of the circumvallate papillæ bear embryonic taste-bulbs at their upper part, but in no instance were any detected in the epithelium of the lateral area of a papilla. The largest number visible in a single vertical section was three, and each of these represented a different stage in development. The bulbs most advanced are spheroidal in shape, and extend, in a vertical or oblique direction, across the stratum of epithelium. Other bulbs, more rudimentary in character, lie partly in the epithelium and partly in the mucosa, and still others appear to be almost wholly subepithelial in position. The largest and most fully developed of these embryonic bulbs measures 0·030 mm. in length and 0·028 mm. in breadth. The nerves, which could only be recognised with great difficulty in the tongue of the fœtus of the fourth month, are here, for the most part, quite clearly shown. Medullated fibres of the glosso-

pharyngeal nerve enter the base of the circumvallate papilla, and soon after divide and subdivide, forming a rather coarse plexus at the upper part of its body. Many of the terminal branches of these fibres have lost their medullary sheath, and can be traced to the upper part of the papilla, while very few apparently are distributed to its lateral area. In the mucosa, directly underlying the deep layer of columnar cells of the epithelium, these nerve-fibrils form a fine delicate network, very similar in some respects to that which I have seen in the papillæ of the common hare (*Lepus americanus*). In the circumvallate papilla of this rodent, owing to my success with gold preparation, I found the subepithelial network very beautifully depicted, the nerve-fibrils and small ganglia, which are scattered through the membranous stroma, being stained deep violet or black. A portion of the terminal fibrils of the network enter the bulbs at their base, while others pass between the latter, and end freely in the epithelium, or possibly form an intra-epithelial plexus.[1]

I failed to discover embryonic taste-bulbs in the foliate organs of this fœtus, but isolated bulbs were present at the upper part of some fungiform papillæ. They are placed vertically in the long axis of the papilla, and are almost entirely epithelial in position. One of the most conspicuous bulbs of this region was pyriform in shape, and measured 0·0185 mm. in its greatest transverse diameter, and was 0·033 mm. in length. The peripheral end of the neck of this bulb failed to pierce the outermost layer of pavement epithelium.

The third tongue which I investigated came from a fœtus at the end of the sixth month. This tongue measures 27 mm. in length, 19 mm. in breadth, and 8 mm. in thickness, and is free from the floor of the mouth for 8·5 mm. The papillæ, which can now be seen without the microscope, are distributed quite uniformly over the dorsum, and those of the fungiform variety are quite numerous near the lateral margins and upon the anterior third and tip of the organ. Some of those of the tip are encircled by a deep fossa, and in vertical sections bear a

[1] Drasch has described in detail, in the treatises already cited, the arrangement and distribution of the nerves in the foliate papillæ of the rabbit and hare. A discussion of the results of his investigations, and his deductions therefrom, would lead me beyond the scope of this paper.

striking resemblance to normal circumvallate papillæ. The papillæ of mechanical function are quite thickly placed at the fore part of the dorsum. They consist largely of conical or cylindrical-shaped elevations of the mucosa, and are covered with a thin stratum of pavement epithelium. They measure about 0·20 mm. in height, and from one-third to one-half as much transversely. The lingual epithelium has increased in thickness, and proliferation of its cells is still very active. In the mucosa and submucosa fat is quite abundant. It is mostly in the form of closely aggregated circumscribed groups of fat cells.

At the back of the tongue, and disposed somewhat in the form of a crescent, are eight circumvallate papillæ. These papillæ are not all equally advanced, but they are all lobate or compound, varying in the number of their lobes from two to eight. The epithelium covering their upper surface is thicker and more substantial than that of the lateral area. The papillary and outer wall of the trench are not yet in all cases completely differentiated, but in many of the papillæ the trench is open throughout its extent, although still very narrow. Some of the papillæ possess secondary ones, the depressions between them being filled with pavement epithelium. Serous glands are plentiful, and their ducts communicate directly with the trenches, opening into them either at the base or sides. Mucous glands are also present, but they are situated in this region externally to the serous glands, and somewhat nearer the under surface. The circumvallate papillæ vary greatly in their dimensions, depending on the number and size of their respective lobes. One measured 0·35 mm. in breadth and 0·30 mm. in height; whilst another, with three large and nearly equal lobes, had a transverse diameter of 1·20 mm.

The foliate papillæ are still in process of formation, and are less advanced than those of the fungiform or circumvallate type. Each papilla consists of six to eight folds, which differ greatly in size, shape, and appearance. Many of the folds are cleft vertically, often in several places, the clefts being wholly or in part filled with fusiform cells of the epithelium. At the anterior limits of the foliate organ the mucous membrane is thrown into a lineal series of fairly uniform papillary elevations. These

elevations are rounded at the summit and slightly constricted near the middle, and measure on the average about 0·34 mm. in height and 0·10 mm. in their greatest transverse diameter.

I will observe here that it is by no means always an easy matter to define with exactness the anterior limits of the foliate organ in man. The nearest approach to the foliate type is probably reached in later fœtuses and very young children. In man the characteristic primary and secondary lamellæ of the typical foliate organ are either wanting or imperfectly developed, and the presence of taste-bulbs may or may not be of diagnostic value in determining the nature of the organ in question.

The epithelium covering the upper surface of the folds of the foliate papillæ is thicker than that of the sides, and measures 0·045 mm. in thickness. The furrows are not yet entirely free from epithelium, but the latter is for the most part confined to their lower half. Within the folds are small collections of fat cells, deposited in spheroidal or oval-shaped masses, and about their bases are serous glands and ducts in abundance.

Taste-bulbs are not very numerous in the circumvallate papillæ. They are most frequent on the exposed surface, although they occur to some extent in the epithelium of the lateral area. They measure on the average 0·039 mm. in length and 0·024 mm. in breadth. In the foliate organ the bulbs occur on both the free area and sides of the folds, but they are smaller, fewer in number, and more subepithelial in character and position than those of the circumvallate papillæ. Some of the taste-cells of a bulb were isolated sufficiently for partial study. They are long and narrow, and terminate peripherally in a very minute point. In the nuclear region of the cell they measure 0·0025 mm. in diameter. The nucleus is oval in form, and is situated in the lower half of the cell. The central end of these cells was lost in the stroma of the mucosa. Bulbs were rarely met with in the fungiform papillæ, and those that were seen were rudimentary in character.

In the anterior region of this tongue, a little back from the tip and near the lower surface, I found the mucous glands of Nuhn. They were well developed, and their ducts opened on the under surface of the organ.

The fourth tongue worked upon came from a fœtus of the

seventh month. It measures 35 mm. in length, 17 mm. in breadth, and 14 mm. in thickness. Anteriorly it is free from the floor of the mouth for 10 mm. The upper surface is faintly impressed with a medial groove. The tip, which is expanded and flat, is beset with long, coarse, closely aggregated papillæ of various shapes. The mucous membrane of the anterior surface is in places thrown into fairly uniform elevations, varying somewhat in size, but resembling a series of loops. Fungiform papillæ are fairly numerous, and are most thickly distributed over the anterior third, and upon the sides of the tongue. Those about the tip are elliptical in form, and are joined to the tongue by a narrow pedicel. They measure about 0·33 mm. in height, their greatest transverse diameter being 0·15 mm. The extreme posterior dorsal surface of the tongue is obliquely furrowed, and projecting from it are quite a number of coarse, fleshy elevations, the apices of which are directed inwards and backwards. The subparallel transverse folds of mucous membrane of the lateral edges of the organ stand out prominently in this tongue. Beginning at the anterior limit of the foliate papilla they gradually decrease in size, and cease altogether just before reaching the tip of the organ. Near the lateral border on either side of the tongue, a little beyond and in line with the outermost circumvallate papilla, is an epithelial-lined recess, the floor of which is invaginated upwards into a ridge. I was at first disposed to regard these depressions of the mucous membrane as mucous crypts, but their size, position, and structure rendered this supposition doubtful, and upon a closer inspection of them I was led to conclude that they were not.

Two fœtuses of this period of intrauterine life came under my observation, and each of them possessed eight circumvallate papillæ. In both, seven out of the eight papillæ were lobate. They are disposed on the tongue very much as in the new-born child, and rise slightly above the level of the general lingual surface. They vary greatly in size, and are still more or less embryonic in character. One of medium proportions measured 0·65 mm. transversely and was 0·28 mm. in height. The epithelium protecting their upper surface is a trifle thicker than that covering the sides. The trenches vary in depth and width in different papillæ, and in some instances are still undif-

ferentiated in their whole extent. Serous glands are plentiful beneath the papillæ, and frequently project between them, and more rarely extend into their interior. They form a broad belt stretching nearly across the tongue in this region, the continuity of which is here and there interrupted by bundles of muscular fibres. A band of fine and exceedingly delicate wavy fibrils of connective tissue, 0·060 mm. in breadth, extends transversely across the tongue in the anterior part, separating completely the mucosa and muscular layer.

The papillæ foliatæ consist of seven or eight folds, the largest and most developed of which are situated at the posterior limits of the organ. Some of the folds are cleft into secondary ones, the depressions between which are filled with stratified pavement epithelium. A few of the furrows are still partially filled with epithelium.

This fœtal tongue offered more favourable conditions for studying the finer structure of the taste-bulbs and nerves than any of those previously examined.

The bulbs have increased greatly in number, but in their disposition they are yet very unsymmetrical and irregular. They still occur most frequently on the upper area of the papilla, and in this region their development is furthest advanced. Other bulbs, more embryonic in character, are scattered at irregular intervals around the sides, the uppermost tiers containing the most mature bulbs. In some circumvallate papillæ bulbs are wanting altogether on the lateral area, and now and then entire papillæ will be destitute of them. I have frequently found them occurring on the opposed wall of the vallum, situated usually in the upper part. Two bulbs were embedded in the lingual epithelium beyond the outer wall of the trench. They were placed obliquely to the underlying matrix of connective tissue, with their apices directed inwards. One of the most mature bulbs of this tongue measured 0·048 mm. in length and 0·036 mm. in breadth. Horizontal sections through the crest of one of the circumvallate papillæ showed it to be crowded with bulbs. I counted forty, but they exhibited the greatest difference in size and form, and many of them were partly subepithelial in position.

In the foliate organ the taste-bulbs are restricted to a few

folds, and are smaller, fewer in number, and less advanced structurally, than those of the circumvallate papillæ. Only a few folds bear bulbs on both their upper and lateral areas. The fungiform papillæ of the anterior third and tip of the tongue contain fairly well developed taste-bulbs, and the latter are not infrequently more advanced structurally than the papillæ which bear them. One bulb lying at the upper part of a fungiform papilla (which was situated directly on the tip of the tongue) measured 0·045 mm. in length and 0·030 mm. in breadth.

Bulbs were seldom met with on the epiglottis. A few were present in the lower part of the posterior surface, and I found one on the anterior surface. They lie deeply embedded, and are small, spheroidal, rudimentary structures. In the soft palate and uvula of one of the seven months' fœtuses were several small bulb-like bodies. In a vertical section through the anterior part of the soft palate I found a single bulb, lying mostly in the epithelium, with its apex projecting slightly beyond the free surface of the latter. This appearance of the apex was doubtless due to the superficial layers of epithelium having become detached. This bulb resembled those of the epiglottis, and measured 0·035 mm. in length and 0·025 mm. transversely. Of the bulbs of the uvula, also epithelial in position, the most conspicuous measured 0·027 mm. in length and 0·019 mm. in breadth. Mucous glands were present in this region.

Transverse and vertical sections through the taste-bulbs show that the number of taste or sensory cells has, by most observers (Hermann alone excepted), been considerably underestimated. In a transverse section of a bulb (measuring 0·028 mm. in diameter) which passed through the nuclei of its component cells, I counted twenty-three sensory cells. From an examination of many sections I think the mean number of these cells is about sixteen. Two kinds of sensory cells are distinguishable. The first kind comprises the taste-cells of Lovén, with which the *stiftchenzellen* of Schwalbe are identical. The second kind, which are less numerous and less highly refractive, are those designated by Schwalbe *stabzellen*. There are other cells which do not appear to exactly agree structurally with either of the above, but these I am disposed to regard as inter-

mediate or degenerate forms of the needle-cell or staff-cell. A third element which enters into the construction of a taste-bulb is an intercalary network composed of very delicate filaments, through the meshes of which the sensory cells pass. Whether this intra-bulbous network springs from the intra-epithelial or subepithelial plexus I was unable to determine, though I am inclined to believe that it is derived from the latter.

Medullated nerve-fibres enter the circumvallate papilla through its pedicel. These divide into smaller ones, and some of the finer branches subdivide beneath the epithelium into a number of terminal fibrils. In the earlier stages of embryonic and fœtal life these ultimate nerve-fibrils, as already pointed out, are more numerous at the summit of the papilla. In the later periods, however, they also stream towards the sides bearing taste-bulbs. From the delicate network, directly beneath the basal layer of epithelium, fibrils run to the bulbs, and also pass into the epithelium in the spaces between them. Precisely how these intra-epithelial nerve-fibrils terminate in all cases I unfortunately did not succeed in discovering. The very delicate intra-epithelial network which I had failed to detect in earlier fœtuses was in this fœtus quite well shown. It is far more probable that the terminal fibrils, or at least a portion of them, contribute to the formation of this network, than that they enter the bulbs laterally, as supposed by some observers.

The sensory cells of the taste-organs are, I believe, unquestionably developed directly from the peripheral extremities of the nerve-fibrils, this development taking place somewhat in the following way:—The incipient stages of growth are more or less completed in the mucosa beneath the epithelium. The fasciculi of nerve-fibrils, as they become more organised, penetrate the deep layer of epithelium, the columnar or basal cells of the latter being gradually forced asunder owing to the pressure exerted by the inpushing bulb. These cells, which become elongated, and gradually modified into spindle-shaped ones, proliferate into the mucosa, and are partially reflected over the nerve-cells before the latter have entirely embedded themselves in the epithelium. Ultimately they form the peripheral envelope of the bulb, and function as supporting and protecting elements. The sensory cells are not completely covered until

somewhat later, for in several bulbs lying wholly within the epithelium they can still be detected through the little chinks separating the opposed edges of the modified epithelial cells.

If the foregoing explanation of the genesis of the taste-bulb be the true one, as my experience would lead me to infer, the sensory elements of the bulb are derived from the epiblast and not from the hypoblast as supposed by some, although, of course, if the epithelial covering of the tongue be hypoblastic in origin, the peripheral cells of the bulb would spring from that.

Coming now to the newly-born, we find in a child twenty-eight days' old all of the circumvallate papillæ completely differentiated. The epithelium covering them is well organised, and their expanded summits are subdivided into many secondary papillæ. The serous glands are well developed, and here and there the ducts open directly on the free lingual surface. Where two papillæ share an enclosing wall in common, the bottom of the mid-trench separating the opposed walls of the papillæ is frequently invaginated upwards into a ridge. At the sides of the ridge serous ducts discharge. All of the circumvallate papillæ bear taste-bulbs, though not all of the lobes of an individual papilla. Isolated bulbs still occur on the free upper surface, but they are usually situated near its outer limits. The bulbs are disposed quite regularly at the sides in five to eight tiers, those of the uppermost tier being the most mature. In the upper tiers the peripheral processes of the taste-cells of several bulbs project from the pore, whilst in the lower ones many of the bulbs are still partly subepithelial in position. A typical taste-bulb of this child measured 0·057 mm. in length and 0·033 mm. transversely. Bulbs, although not abundant, are present on the posterior surface of the epiglottis.

In a child of seven weeks all of the seven circumvallate papillæ save one were lobate. The fungiform papillæ were relatively larger than in the adult. The orifices of the mucous crypts on the posterior dorsal surface of the tongue were easily distinguishable with an ordinary pocket-lens.

In a child four months' old only one of the circumvallate papillæ appeared to be lobate. The taste-bulbs have increased in size and number. In one horizontal section I counted seventy-

six bulbs, the mean of the different levels being about sixty. They are quite uniformly disposed at the sides of the papillæ, those of the lower tiers being less regular in arrangement and smaller, and lying partly in the mucosa. The most mature bulbs have a number of hair-like processes protruding through their taste-pore for a distance of 0·0035 mm. The largest bulbs measure about 0·069 mm. in length and 0·033 mm. in breadth, the average being considerably less. Serous glands and ducts are very plentiful, there being sometimes more than a score of the latter visible in a single section of a papilla. A circumvallate papilla cleft into two unequal lobes, and with its summit much below the plane of the general lingual surface, almost completely fills the foramen of Morgagni. This papilla is very rich in taste-bulbs. There are many in the epithelium of the upper and under surface, and the lateral area is crowded with them. The perpendicular wall of the foramen cæcum, corresponding to the outer wall of the trench, also bears many bulbs at its upper part. Serous and mucous glands are present in abundance, and the ducts of the former discharge into the foramen cæcum at various places. The folds of the foliate papillæ, eight or nine in number, are very irregular, but the furrows are free from epithelium. Bulbs are sparingly present on the upper surface, and have increased in number on the lateral area of the folds; but their disposition in both regions is far from regular, entire folds often being destitute of them.

With the object of comparing the taste-organs of very young children with those of full-grown individuals, I examined quite a large number of human adult tongues. The circumvallate papillæ of these tongues varied in number from seven to ten, the average being eight. More than half of the tongues possessed lobate papillæ, and in a few instances the latter were verrucose on top. I am inclined to believe that lobation of the circumvallate papillæ is a more distinctively characteristic feature in man than in the lower animals. It is certainly one less commonly met with in those which I have investigated, some twenty-five species in all.

In none of these tongues, which were from individuals presenting a considerable range in age, did the bulbs of the circumvallate papillæ appear to be perceptibly decreased in number,

although they had disappeared almost entirely from the upper surface. In horizontal sections I have seen a hundred or more, forming a zone around the papilla. In most of them the neck (or canal leading down to the bulb, as the case may be) is clearly shown, and in a number of instances nerve-fibrils can be traced directly to their basal end, with which, to all appearance, they are continuous. They vary in shape and size, some of them having the form of a peg-top, and measuring only 0·048 mm. in length and 0·033 mm. in breadth. In the circumvallate papilla, which springs from the floor of the foramen cæcum, I found bulbs plentiful, but they were small and confined to the lateral area.

In the foliate papillæ of the adult only a few folds ordinarily bear bulbs, and I have examined adult foliate organs without finding even a vestige of them. They occur on the free surface as well as on the sides of the folds, and measure 0·07 mm. in length and 0·038 mm. in breadth. I explored the folds of the posterior dorsal surface, and also various other regions of the tongue, with the hope of exposing taste-bulbs, but I failed to discover any trace of them. In the lower part of the posterior surface of the epiglottis, however, I found quite a number of bulbs. They are placed some distance apart, and the majority still retain the spheroidal shape. They measure 0·048 mm. in length. Another form, of which there were a few examples present, measured 0·060 mm. in length and 0·048 mm. in breadth.

SUMMARY OF RESULTS AND CONCLUDING REMARKS.

On the tongue of a human fœtus, at the fourth month of intrauterine life, are five papillæ of the circumvallate type. These papillæ are in process of formation, and illustrate the earlier stages of development, those most advanced being still very embryonic in character. There are no trenches, properly speaking, but their future position is indicated by the prolongations of the epithelium into the connective-tissue matrix of the tongue. One of the smaller papillæ of this fœtus bears on its exposed surface an embryonic taste-bulb. This bulb lies directly in the longitudinal axis of the papilla, and its base is

hidden in the mucosa. Elsewhere in these papillæ were unmistakable evidences of structural modifications, both in the basement layer of epithelium and in the underlying tissue. These changes were of a nature to suggest the incipient stages in the development of the taste-organs.

On the tongue of a fœtus, at the middle of the fifth month, are six circumvallate papillæ, some of which are lobate. One or two of these papillæ are in process of transition from the fungiform type. The trenches are not yet differentiated, and the structural continuity between the epithelium investing the free area of the papilla and that covering the general lingual surface is still unbroken. The foliate organs, which I failed to detect in earlier fœtuses, consist of a few folds of the mucous membrane, the place of the future sulci being indicated by the epithelial ingrowths which at intervals penetrate the mucosa. The majority of the circumvallate papillæ bear embryonic taste-bulbs on their exposed surface, the largest number visible in a single vertical section of a papilla being three. The more advanced among them are mainly epithelial in position, while the less mature are largely embedded in the stroma of the mucosa. Medullated nerves are fairly shown in these papillæ. The main trunks divide in the papillary axis, and form a primary plexus. Directly beneath the basal cells of the epithelium is a fine, delicate reticulated network, from which non-medullated nerve-fibrils pass upwards, penetrating the bulbs and neighbouring epithelium. No taste-bulbs were seen on any part of the lateral area of the circumvallate papillæ, and none were discovered in the foliate organs, but many fungiform papillæ bore them at their upper part.

On the tongue of a six months' fœtus are eight circumvallate papillæ, all of which are lobate. These papillæ are not all equally advanced, but in most of them the structural continuity hitherto existing between the epithelium covering their upper area and that overlying the adjacent lingual surface has become interrupted. The papillary wall and outer wall of the trench of the different papillæ have for the most part separated, leaving a very narrow fissure. Taste-bulbs are most frequent on the upper area of the papillæ, but a few immature ones are sparingly scattered over the lateral walls. The foliate organs consist of

six to eight very irregular folds, several of which are cleft vertically. The furrows, like the trenches, are open throughout their extent. On the folds of the foliate organ there are a few taste-bulbs scattered over the upper surface and sides, but they are small and partly subepithelial in character. In the anterior region of the tongue, not far from the tip and under surface, are the mucous glands of Nuhn, with their ducts opening on the lower surface of the organ.

On the tongue of a fœtus at the seventh month are eight circumvallate papillæ, all but one of which are lobate. In a few instances the trenches are not completely differentiated, and some of the furrows of the foliate organs are partially filled with epithelium. The taste-bulbs have increased greatly in number on the lateral area of the papillæ, and have not decreased apparently on their upper surface. Those situated at the lower part of the papillæ are, as a rule, the smallest and least advanced. Bulbs are present on the outer wall of the trench, and even occur beyond it embedded in the lingual epithelium. Many of the bulbs of the circumvallate papillæ lie partly in the mucosa, and the ultimate nerve-fibrils or filaments, which constitute the sensory elements of these terminal organs, can be seen within the epithelial shell, where the cells of the latter have been but partially reflected over them, or where the imbrication is incomplete. In the foliate organs bulbs occur on the summit and sides of a few folds. They are also present on the anterior and posterior surface of the epiglottis, and in the epithelium of the soft palate and uvula.

In a child about a month old the taste-bulbs had increased in number, and isolated ones still occurred on the free upper surface of the papillæ. In the lower tiers of the lateral area many of the bulbs were still partly subepithelial in position.

In a child four months old the papilla of the foramen cæcum bore bulbs on its entire exposed area, they being likewise present in the wall facing the papilla.

In the circumvallate papillæ of the adult the taste-bulbs do not appear to have decreased in number, although they have disappeared almost completely from the upper surface. In the foliate organs they are less numerous than in early life, but are still normally present on the lateral and upper area of the folds.

From a study of the gustatory papillæ of the different fœtuses, it appears highly probable that the nerve-fibrils given off from the network beneath the epithelium of the bulb-region of the papilla terminate either as specialised end-organs of taste, or penetrate the epithelium, to all appearance unchanged. Those fibrils which are to compose the future sensory elements of the bulbs form themselves into fasciculi of delicate filaments, the latter becoming more or less modified before penetrating the epithelium. While these changes are taking place in the mucosa there is an increased activity manifested by the contiguous basal cells of the epithelium. These become swollen and elongated, and grow downwards and inwards, gradually enveloping the newly-formed terminal organs. Eventually these cells constitute the intercalary and peripheral cells of the bulbs. A portion of the non-medullated nerve-fibrils which enter the epithelium directly doubtless take part in the formation of the intra-epithelial network. Other fibrils appear to end freely in the epithelium.

There has been a tendency on the part of nearly every investigator of the gustatory terminal organs to underrate the number of taste-cells. From my own criteria, I should place the number of sensory- or nerve-cells in a bulb of average size and maturity at sixteen; and I think that this estimate cannot be very wide of the truth.

I cannot entirely agree with those histologists who are disposed to multiply the kinds of taste or sensory cells, and I frankly admit that, after a careful search, I was unable to distinguish more than two distinct forms of these elements. The first form is identical with the taste-cell of Lovén (needle-cell of Schwalbe), to the description of which I have nothing to add. The second form, answering to the staff-shaped cell of Schwalbe, is larger, less frequently met with, and less highly refractive than the former, and, moreover, lacks the styliform process. The staff-shaped cells possess a large ovoidal body, situated in the lower half of the cell, and are usually placed more externally than the cells of Lovén, the latter having a tendency to group themselves nearer the axis of the bulb. A third element which enters into the construction of a taste-bulb is a fine network, composed of very delicate filaments, through the meshes of

which the sensory cells pass, and which may be derived from the subepithelial plexus.

It is not altogether unlikely that insufficient allowance has been made for differences in the structural details of individual cells. I have occasionally observed elements within the bulb which failed to agree structurally with either recognised form of taste-cell, but I have been inclined to look upon them as representing intermediate stages of regeneration or degeneration, as the case may be, of either or both kinds of taste-cells; and what is observed may be either the initiatory stages of cells in process of growth or the vestigial products of degenerated ones.

Some time prior to the investigation under consideration I had, from *à priori* reasoning, adopted the view of the subepithelial nature of the sensory elements of the taste-bulb, it having commended itself to me as the most acceptable explanation of the many perplexing and seemingly contradictory phenomena with which investigators of these terminal sense-organs are frequently confronted. And I had, moreover, felt assured that if it could be shown that the bulb, at any stage of its existence, was largely subepithelial in position, the subepithelial nature of its sensory cells would not be seriously questioned. Griffini has already demonstrated by physiological methods the subepithelial character of the taste-cells, and my own results coincide essentially with his. I have no wish to be understood as denying the existence in these organs of neuro-epithelial cells, only I have never knowingly observed them, and can see no obvious necessity for their presence.

Poulton[1] was the first, I believe, to direct attention to the subepithelial nature of the taste-bulbs. He based his conclusions on the appearance of these organs as presented in *Perameles*, but more especially in the ancestral *Ornithorhynchus*. In the latter type he discovered bulbs wholly embedded in the mucosa. In the case of the higher mammals this author conceived that the primitive terminal organ of *Ornithorhynchus* was replaced by one epithelial in character. That this is not, however, necessarily so I have endeavoured to show. The bulb as a terminal organ has

[1] *Quart. Jour. Micr. Sci.*, vol. xxiii. p. 470, 1883.

undoubtedly, in passing from lower to higher forms, become more highly specialised and consequently more complex, but in all likelihood its nature and mode of origin have remained essentially unchanged. Poulton, in discussing the origin of the taste areas of mammals, is inclined to regard the gustatory ridge of *Ornithorhynchus* as an intermediate form between the circumvallate and foliate types,[1] rather than as a precursory type of bulb-bearing organ.

The hypothesis that a fungiform type of papilla is always a forerunner of the circumvallate form, and that all circumvallate papillæ are but modifications of the fungiform type, is, I think, scarcely tenable. While some circumvallate papillæ unquestionably arise in this way, others, probably the greater number, have an independent origin.

What purpose the temporary taste-bulbs (for such they seem to be) of the free upper surface of the circumvallate papillæ subserve in the embryo is difficult to comprehend. With the appearance of the bulbs of the lateral area they gradually disappear, and, from all indications, perish. By the time the bulbs of the free surface of the papillæ have attained their full development, bulbs in early stages of formation make their appearance on the wall, the lowermost bulbs being the most elementary. Were it otherwise it might be conceivable, as Hermann suggests,[2] that by an unfolding of the papilla laterally the bulbs of the free area are shifted to the sides. In the present state of our knowledge there seems to be no better way than to believe with Hoffmann,[3] that "the bulbs of the free surface perish through the proliferation of the ordinary epithelium." It is not improbable that after the bulbs have once disappeared from the upper surface that certain altered conditions of the epithelium prevent, save in rare instances, their recurrence there.

Klein[4] has observed that in newly-born children, owing to the indistinctness of the wall in most instances, no difference is perceptible between the circumvallate and fungiform papillæ. This statement must have, I think, a somewhat restricted

[1] *Loc. cit.*, p. 471. [2] *Loc. cit.*, p. 228 *et seq.*
[3] *Loc. cit.*, p. 528 *et seq.*
[4] Stricker's *Manual of Histology*, New York, 1872, p. 353.

application, for not only in tongues of new-born children, but in those of fœtuses of six and seven months the two forms of papillæ are readily distinguishable from each other, and by means of the glass can be recognised at still earlier periods of intrauterine life.

While it is possible to study the succeeding stages in the development of the taste-bulbs during the latter period of intra-uterine life, and consequently to learn something of the different elements of which they are composed, yet the first appearance of the taste-organs of man must be sought in earlier embryos than those examined by me.

NOTES OF A CARDIAC NEUROTIC.

By Dr C. HANDFIELD JONES.

THE heart is the most vital and laborious organ in the body; consequently, any even slight disorder or failure of its normal action, such as would be quite insignificant in any other muscle, is not unworthy of the physician's attention lest it grow to greater gravity, and threaten even life itself. Moreover, by study of the lesser derangements we may attain to a better comprehension of the greater. Thus much may be said in justification of the following notes:—

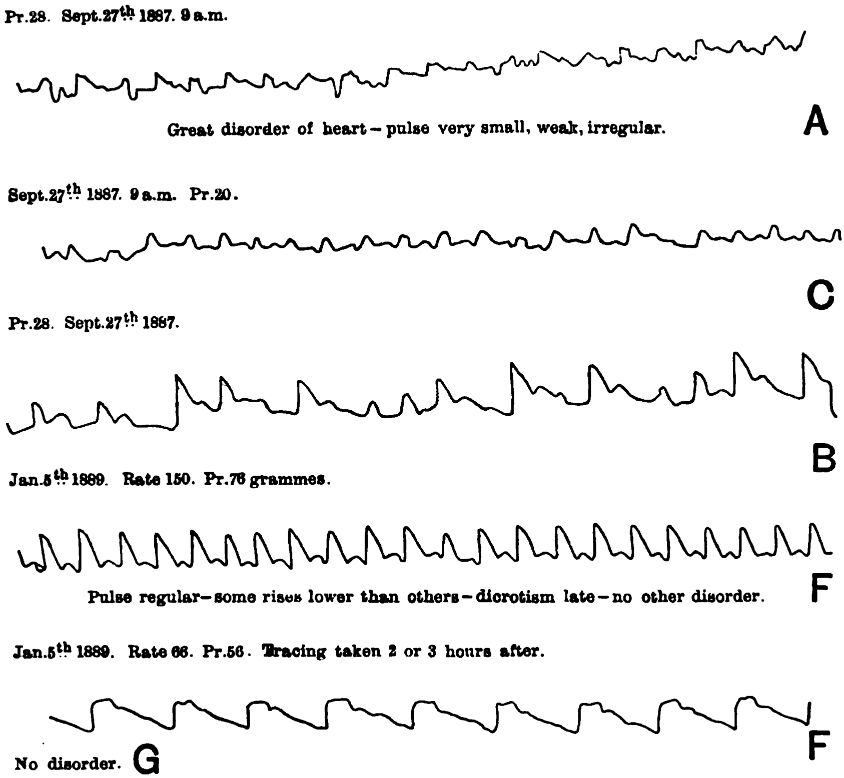
On the morning of September 27, 1887, X. Y., æt. 70, felt all right while dressing until he made some extra exertion, but only such as he had very frequently made before without any ill effect, and has since. Soon after this he felt rather queer, and found his pulse exceedingly small, weak, and irregular. This state continued for an hour or so with little change, in fact during most of the forenoon, but gradually subsiding. He felt rather faint now and then, but did not look pale. Much flatulence escaped at intervals, with some relief, but not more than had often existed harmlessly. The deranged cardiac action is well shown in several tracings which were taken about 9 A.M., some thirty minutes after the attack commenced. The characters of the four first are striking smallness and irregularity, with markedly flat tops in two, and numerous small undulations on the descent, which terminated sometimes in a sudden drop below the base line. About 1 P.M. the primary rise of the tracings became higher and more vertical, but the amplitude varied greatly, and the general form resembled very much that of the tracing of some hypertrophied and dilated hearts. After an hour's languid walk the tracing was quite regular, with round or flattish tops, early and slight dicrotism, in fact was pretty normal, allowing for senility. In about nine hours from its onset the disorder had ceased without the administration of any remedy. It was clearly functional. The only probable cause to which the derangement can be attributed is the somewhat too

free indulgence in tea, which had been permitted for two or three weeks previous.

On October 16, just after a quite small dose of tea, the same individual found his pulse in about an hour so small, quick, and irregular, that it was often hard or impossible to feel it. It remained in the same state about an hour, then became gradually slower, more distinct, and regular, and soon was normal. The heart's action was at first excited, as if it were struggling against an obstacle, and its impulse was more evident to its owner than usual. No tracing was taken on this occasion, but there can be little doubt that the disorder in both was essentially of the same kind. The sensation experienced was not exactly one of faintness, but as if the brain was insufficiently sustained by the circulation, as if the blood-pressure in its capillaries was too low. Since then fifteen months have elapsed without any return of the cardiac or arterial trouble. The heart is fairly valid, and can endure a considerable amount of exertion —even a 30 miles' walk—without any sign of failure. The remarkable smallness of the pulse-tracing A, compared with the much greater amplitude of B, when the disorder on the first occasion was passing off, and the sense on the second of the heart contending against an obstacle, suggest the idea that the peripheral arteries were unduly contracted; that the attack, in fact, was of the nature of angina pectoris—a tendency to which is hereditary.

Towards the end of August 1888, X. Y., after some slight lumbago, took a morning cold plunge-bath, as he often did. On returning from the bath to his dressing-room, up three flights of stairs, his heart's sounds were found on auscultation very loud, running together, and so very harsh as to suggest strongly to the observer the existence of pericardial friction: the action was very quick. In about five minutes the rate was slower, the sounds much less loud, the first pause evident, the action calmer. The bath had certainly often been taken before without such results. It is probable that the sudden application of cold to the cutaneous surface caused reflexly over-contraction of the arteries generally, which hindered the blood from passing on freely, and so produced undue pressure on the inner surface of the left ventricle, and stimulated it to contract more forcibly.

Had the heart's tissue or valves been unsound the results might have been more serious. Perhaps the sudden death of capable swimmers may occasionally be brought about in the same way.



A. Tracing of September 27, 1887, Pr. 28, small, irregular, flat-topped in several beats.

C. Tracing at same period, probably rather later, tops less flat, Pr. 20.

B. Tracing during recovery much more ample, but unequal, Pr. 28.

F. Tracing of rapid pulse, tops pointed, dicrotic notch late, Pr. 76.

G. Tracing of pulse some hours later; shows senile character, Pr. 56–80.

On January 5, 1889, soon after his usual breakfast of coffee, bread, and meat, X. Y. found his pulse going at the rate of 150 per minute, quite regular, as shown by the tracing, though it did not feel so to the finger, and giving a fair rise (·2 inch), with pressure of 80 grammes. The dicrotic notch was very late, mostly at the base line. The top was pointed. There was some flatulence. In two or three hours the pulse-rate fell to 66, and the tracing resumed its usual form, with a broad flat top and early dicrotism. The tracing A is extremely unlike F, the former manifestly indicating a hard, the latter a soft pulse. It is not possible to determine whether the rapid action is to be attributed to excitation of the accelerator nerves of the heart or to paresis of the cardiac vagi, but considerations, presently to be mentioned, induce me to think the latter most probable. The chief interest of the case appears to me to consist in the evidence it affords that an artery habitually in a state of undue tension can be changed into one of collapsing character by an influence which can only be regarded as due to altered innervation. What that influence was cannot be known; but as pyrexia, external heat, and strong exercise enfeeble nerve force vascularly as well as generally, it may be presumed to have acted in a like way. Moreover, failure of nerve force is a more probable occurrence than excitement, apart from special motors.

ADDITIONAL OBSERVATIONS UPON THE INTRA-NARIAL EPIGLOTTIS.[1] By G. B. Howes, F.L.S., F.Z.S., *Assistant Professor of Zoology, Normal School of Science and Royal School of Mines.*

(*Continued from page 272.*)

SINCE writing my previous paper on the above subject, there have come under my notice two important monographs thereon by Rückert[2] and Waldeyer,[3] and I have had opportunity (thanks largely to the liberality of my friends) of examining important material hitherto inaccessible to me. As certain of the facts which have revealed themselves are deserving of special mention, I proceed to the consideration of them; and I take the opportunity of appending a classified list, with references, of all mammals in which the intra-narial epiglottis has been observed, in the hope that it may be of service to future investigators.

1. PRIMATES.

I showed in my previous paper (this vol. p. 267) that the intra-narial epiglottis had been observed *post-mortem* in representatives of all orders of mammals, with the exception of the *Primates*, *Hyracoidea*, and *Sirenia*.[4] In the discussion which followed the reading of the paper, Professor Macalister observed that he possessed a section of the human pharynx, in which the epiglottis and velum palatinum were both seen.[5] Professor Bland Sutton, at the same time, called attention to the fact that he had detected the truly intra-narial condition in the human fœtus at five months and at birth. To the fuller consideration of Professor Sutton's observations I shall return. It is more

[1] Read before the Anatomical Society of Great Britain and Ireland, March 1889

[2] *Der Pharynx als Sprach- und Schluckapparat.*, J. Rückert, München, 1882.

[3] *Sitzungsb. der König. Preussch. Akad.*, Berlin, 1886, pp. 233–250.

[4] The *Cheiroptera* and *Monotremata* were originally added, in ignorance of the fact (with which I have since become acquainted) that Robin and Rückert had already recorded the intra-narial condition in them (*cf.* Table).

[5] In the discussion which followed the reading of this paper, Professor Macalister stated that the section referred to was, upon re-examination, found to be very oblique.

pertinent to point out here that the facts cited for the human subject receive a direct interest from the discoveries of Rückert, who, of all observers, has paid most attention to this question. He has concluded,[1] from an elaborate study of the comparative anatomy of the pharynx in the leading orders of mammals, that in Man and most anthropoid Apes the parts are (in contra-distinction to that which is seen in other mammals) so disposed that the velum palatinum does not reach the apex of the epiglottis when the mouth is closed. Waldeyer, who next took the subject in hand, substantiated, in the main, Rückert's deduction; he showed, further, that in the young Orang the velum (*loc. cit.*, p. 239) "ohne jede Andeutung eines Zäpfchens,[2] ragt fast bis zum Zungengrunde vor der Epiglottis hinab."

The discoveries here cited call for further inquiry into the behaviour of the epiglottis and velum of the human adult; but in view of them it is clear that, at any rate in the young state, the intra-narial condition of the first-named, predominant among the lower types of mammals, may obtain.

As to the Primates generally, examination of the list which I append will show that the intra-narial epiglottis has now been observed in a series of forms fairly representative of the order. I have been enabled to extend the observations of my predecessors to the *Lemuroidea*. The parts, as seen in the Tarsier, call for no special comment; the epiglottis is a miniature of that of Man, and the arytenoids are not prolonged. In *Lemur*, however, the larynx is more modified. The epiglottis, though short, is erected and extended postero-laterally, embracing the arytenoids somewhat in the manner of that of the *Hippopotamus*,[3] except that the whole forms a tubular organ. The upper border of this is closely embraced by the velum palatinum, and the entire apparatus is suggestive of a transition stage in that of such a form as the Mole.[4]

[1] *Loc. cit.*, p. 40 *et seq.*

[2] The uvula of this animal would appear to be subject to no inconsiderable variation. Rückert denies its existence (*loc. cit.*, p. 23), while its presence has been recorded by Bischoff and Chapman (see *Proc. Acad. Nat. Sci. Philad.*, 1880, p. 6), the specimen dissected by the latter being, like that of Waldeyer, a young male.

[3] *Cf.* Clarke, *Proc. Zool. Soc.*, 1872, p. 188, fig. 2.

[4] *Cf. infra.*

2. Eutheria other than the Primates.

I find that Rückert had forestalled me in the discovery of the intra-narial epiglottis in the Rabbit, and that he confirms that which I originally stated concerning the Hedgehog.[1] I was, however, anticipated in the latter, so far as it might appear to represent the first discovery of an intra-narial epiglottis in the Insectivora, by John Hunter, who long ago briefly described the same in the Mole.[2]

I have to add to the list of Eutherioids for which my predecessors claim an intra-narial epiglottis the "Flying Fox," a remarkable Bat from the Solomon Islands,[3] a Seal, Reeves' Muntjac, the Axis Deer, the Musk Deer, the Coney, and the Manatee. Special consideration is necessary only in the two last-named cases, and to these I shall return.

3. Paratheria[4] (*Edentata*).

The intra-narial epiglottis has been described in this remarkable sub-class by Owen, Garrod, Rückert, Waldeyer, and Sutton (*cf.* List, p. 595). As none of these observers have noted the condition in quest in the Sloths, I have specially sought the same, and am able to record it in *Cholœpus*. I have also to add to the *Dasypodidæ* in which it has been observed, the Six-banded Armadillo and the Pichiciégo or Mole Armadillo (*Chlamydophorus*).

The epiglottis is, in the three above-named forms, elongated, and in the first and last-named the arytenoids are slightly prolonged. In *Cholœpus* the mucous membrane surmounting the arytenoids is prolonged forwards and upwards into a couple of folds which lie within the embrace of the postero-lateral borders of the greatly extended epiglottis. By virtue of this the larynx becomes feebly tubular, and it lies well within the narial pharynx, the velum extending outwards and downwards towards the base of the tongue. There is no trace of uvula.

Reference to my list will show that the epiglottis is associated with the narial pharynx alike in the burrowing and omni-

[1] This *Journal*, vol. xiv., 1880, p. 471.
[2] *Essays and Observations*, edited by Owen, vol. ii., 1861, p. 187.
[3] *Pteralopex atrata*, Thomas, *Proc. Zool. Soc.*, 1888, p. 473.
[4] Thomas, *Phil. Trans.*, 1887, p. 459.

vorous Armadillos, in the arboreal and herbivorous Sloths, and in the insectivorous Ant-Eaters. I regard this as a matter of especial importance, inasmuch as, when taken in conjunction with that well known in the Cetacea, it tends to show that the intra-narial condition of the epiglottis is not to be associated either with a definite dietary or mode of life. The discovery, by Robin, Rückert, and myself, of identical conditions in the insectivorous and frugivorous Bats (*Vespertilio* and *Pteropus*) points to the same conclusion.

4. Metatheria (*Marsupialia*).

The intra-narial larynx exists typically, as is well known, in the young of these animals while on the teat. It has been described in adult Kangaroos by Rückert,[1] Poulton,[2] and Waldeyer. I am able to record it for adults of the Vulpine Phalanger and of that rarissima the "Marsupial" or "Banded Ant-Eater" (*Myrmecobius fasciatus*). Of the first-named animal I have examined four specimens. The epiglottis was, in all, erect and tapering, but in only one did it lie actually above the velum.

In *Myrmecobius* the parts are somewhat exceptionally modified. Thanks to Professor Huxley and Mr Oldfield Thomas, I have had opportunity of examining two specimens. The epiglottis is chiefly remarkable for its great increase in transverse diameter and its sharply truncated base. The edge of the velum is much swollen, and its free (? muscular) border extends back posteriorly to the larynx, its opposite limbs uniting behind, so as to enclose a central groove which overlies the aditus laryngis. In one specimen the epiglottis lay free in the floor of the mouth; in the other it was partially inserted into the narial pharynx, in a manner indicative of an attempt at its withdrawal from (or introduction into) the same in death. Except for the fact that the velum had not fused with the base of the tongue, the condition of the parts was very suggestive of that described and figured by Rückert in the Nine-banded Armadillo.[3]

[1] *Macropus*, *loc. cit.*, footnote, p. 44.
[2] *Acrobates pygmæus*, *Proc. Zool. Soc.*, 1883, p. 616.
[3] *Loc. cit.*, p. 43, and fig. 18.

5. Prototheria.

The announcement of the discovery of the intra-narial epiglottis in *Echidna*[1] followed almost immediately upon the publication of my former paper, and this was to me highly gratifying. Thanks to my friend Professor Charles Stewart, I have had an opportunity of examining a specimen which fully bears out the description given. Rückert has described, in *Ornithorhynchus*, one of the most modified conditions of the parts yet observed, viz., that (alluded to above in *Dasypus novemcinctus*)[2] in which the velum becomes confluent with the base of the tongue, whereby the epiglottis is firmly embraced and the orifice of communication between the mouth and œsophagus (sinus pyriformis) is reduced to the minimum. This condition is less marked in the specimens which I have examined, and I conclude, from comparison with Rückert's description, that the parts of the pharynx are, in this animal, subject to individual variation (*cf.* this vol. p. 269).

6. Hyrax and Manatus.

It became obvious, early in the course of preparation of these notes, that the intra-narial epiglottis could be claimed (*cf.* List) for members of all orders of mammals with the exception of the *Hyracoidea* and *Sirenia*. I accordingly sought the two latter with no slight eagerness, and with what result the following will show.

Hyrax.—On searching the literature bearing upon this genus, my suspicions were aroused by the assertion of Brandt,[3] that "die Gaumenfalten treten übrigens stark vor, so dass sie nach dem Tode des Thieres nicht selten Eindrücke auf der Zunge bewirken;" and, on finding that George had detected[4] the presence of a hyo-epiglottidean muscle, my interest heightened (*cf.* this vol. p. 271). I was not disappointed, for in one

[1] Walker, *Studies from the Museum of Zoology in Univ. Coll., Dundee*, vol. i. No. 3, 1889.

[2] *Loc. cit.*, p. 43. The author also describes a similar condition for the Guinea Pig (*Cavia cobaya*).

[3] *Mem. de l'Acad. imp. des Sci. St Pétersbourg*, vol. xiv. No. 2, p. 53, 1869.

[4] *Ann. des Sci. Nat.*, ser. 6, "Zoologie," vol. i., 1875, art. ix. p. 67.

adult and two embryos[1] which I have examined, the epiglottis was seen to overlie the edge of the velum. The former was, in the adult, well developed, and relatively longer than in the young specimens; looked at from below, it was seen to be inclined upwards and backwards, its free border being swollen and slightly indented around the line of embrace by the velum.

Manatus.—The larynx of the adult Sirenian is chiefly remarkable for the rudimentary condition of the velum and epiglottis. Waldeyer, in writing of it, says[2]—

"Der Kehlkopfseingang ist durch die eng aneinanderliegenden beiden Schleimhautfalten, welche die Aryknorpel überziehen, linear geschlossen. Vor ihnen her zieht bogenförmig eine kurze Epiglottis, die sich dicht an dieselben anschmiegt und in der Mitte einen kopfförmigen Vorsprung trägt, der sich genau vor die Spalte zwischen den beiden Aryknorpelwülsten legt. Sonach ist der Kehlkopfseingang stets geschlossen (falls nicht gerade Luft eingezogen wird). Die Epiglottis ist so kurz, dass sie sich gar nicht deckelförmig über den Eingang des Kehlkopfs zu legen vermag, dabei aber so breit, wenigstens mit ihren seitlichen Falten, wie der Zungengrund und Kehlkopf selbst. Das Velum palatinum liegt mit seinem freien Rande unmittlebar dem oberen Epiglottisrande auf. . . . . Man kann hier nicht von einer Bifurcation des Speiseweges sprechen, so dass letzterer rechts und links neben der Epiglottis vorbeiführte, sondern bei Manatus müssen selbst geringe Flüssigkeitsmengen geradewegs über den Kehlkopf hin zum Oesophagus gelangen. Da aber der Kehlkopfseingang in der angegebenen Weise fast geschlossen ist und dabei eine sanft nach hinten abgedachte Fläche darstellt, so ist dem Eindringen von Flüssigkeiten und festen Nahrungsbestandtheilen dennoch wirksam vorgebeugt."

It will be clear, from the above citation, that the parts of the larynx are, in this animal, modified in a direction altogether special and unparalleled among other mammals. Argument from analogy to that which is now known, points to the conclusion that the modifications in question are secondary and correlated with the reduction of the epiglottis, while, from examination of the parts *in situ*[3] we might, arguing from the same standpoint, reasonably expect to find the epiglottis disposed intra-narially in the embryo. My friend Professor W. N. Parker has, very generously, afforded me an opportunity of

[1] Measuring each 5½ inches in total length. They were originally associated with the fœtal membranes described by Huxley, *Proc. Zool. Soc.*, 1863.

[2] *Loc. cit.*, pp. 245, 246.

[3] *Cf.* Murie, *Trans. Zool. Soc.*, vol. viii. part 3, 1872, pl. xxvi. fig. 37.

examining a fœtal male of *Manatus americanus*, measuring 13½ inches in total length. On laying bare the larynx from below, the epiglottis was found to lie, as I had hoped, within the narial pharynx. When viewed from the side, the body of the larynx was seen to be elevated, as in the adult, and so disposed that the glottis lay at the base of the narial pharynx and at right angles to the long axis of the same.[1] The epiglottis, as viewed laterally, was seen to slope obliquely upwards and backwards; while the hinder border of the velum palatinum was, from its point of apposition with the same, recurved in a similar direction, its free edge being upwardly directed (carried up, as it were, as the direct result of the introduction of the larynx into the posterior narial passage).

The condition of the parts in the above-named embryo is thus seen to differ from that of the adult, precisely as it approximates towards that of the type predominant among other mammals. The epiglottis is larger than in the adult, and the velum extends back beyond the limit of its anterior border; the parts are, in fact, in the condition postulated for them above, an argument from analogy to the less modified forms. The *Sirenia* then are no longer to be regarded as exceptional in relation to the point at issue; and, with this, it may be said that the intra-narial epiglottis has been observed *post-mortem* in adequate representatives of *all orders* of living mammals.

7. General.

It is seen that the intra-narial condition of the epiglottis pervades all orders of Mammalia, and it will be clear from the foregoing that, although that organ may, together with associated structures, become specially modified in correlation with a peculiar mode of life (*e.g.*, *Cetacea*), there is no constancy of relationship between the changes which it may undergo and either the mode of feeding or the nature of the food of the animals concerned. On the other hand, there is everywhere manifest an undoubted association of the epiglottis with the velum palatinum for purposes of respiration, exclusively *per*

[1] It is well to bear in mind that when the mouth is closed the aditus laryngis comes to occupy a similar position in all other mammals, whether the epiglottis lies above or below the velum.

nares. The more we study the several orders the more certain does this become, and the association referred to may wellnigh be regarded as diagnostic of the class Mammalia.

In the light of the new facts herein recorded, it may be well to return to the question how far the intra-narial condition may or may not have been the primitive one for the said class. On reference to my former paper, it will be seen[1] that in the Pig the epiglottis would appear not to enter the narial pharynx until some months after birth. Professor Bland Sutton writes me that he has found, in frozen sections of the human fœtus, the epiglottis to be, at "about the fifth month of gestation," situated behind the velum, and that the most marked case which came under his notice was that of "a fœtus at full time." He found, however, that in "some third month embryos there was quite a wide interval between the epiglottis and the velum;" and from these observations he deduces the belief that "the intimate relation between the two parts must be quite secondary." The facts here cited might appear to support this belief, and I certainly know of none more forcible in that direction.

There has appeared subsequently to the issue of my first paper a valuable monograph by Dr G. Killian,[2] in which it has been shown incidentally[3] that the epiglottis of the Pig is disposed intra-narially *in utero*, at a stage when the embryo measures but 6 cm. in length; and I have quite recently examined a Pig at 5–6 months, in which (unlike that observed by Bowles) the same condition obtained. This being so, the argument in favour of the belief referred to above, so far as it may be adduced from the study of the Pig, breaks down. Against that drawn from the study of the human subject there must be set the structural relationships of the parts in the lower orders of Mammals, the early acquirement of the intra-narial condition in the embryos of certain of the same; and last, but not least, the facts herein recorded for the Sirenia. Consider-

[1] This vol. p. 269. The references given on the same page to Dr R. L. Bowles' papers should read as follows:—"Further Observations on Stertor," *Proc. Med. Chirurg. Soc.*, vol. vi. p. 291, 1871; and "Stertorous Breathing in Apoplexy," *British Med. Jour.*, vol. i. p. 845, 1881.

[2] "Über die Bursa und Tonsilla pharyngea," *Morpholog. Jahrb.*, vol. xiv. pp. 1–96, 1888.

[3] *Loc. cit.*, p. 46, fig. 27.

ation of these weighs heavily against the supposition that the introduction of the epiglottis into the narial pharynx can have been a secondary process. The facts, when viewed in conjunction with those recorded on a previous page, point much more forcibly to the conclusion that such introduction was primary, and that in the call for the same we have the most satisfactory *raison d'être* for the development of the velum palatinum; while, from all that is known, it appears most probable that the latter may have originated in correlation with the conditions of lactation.[1]

In dealing with the question at issue it appears to me necessary to allow for wide individual and specific variation (*cf.* *Ornithorhynchus* and *Sus*, *ante*), and, from what I have seen, I incline to a belief in an occasional temporary arrest in development of either the epiglottis or velum under correlation of growth. The data at our disposal do not warrant any very definite statements concerning this, but it is well to reflect on the demonstration of an allied phenomenon[2] in the temporary occlusion of the œsophagus during transformation of the visceral pouches.

My best thanks are due to my friends Professors C. Stewart and W. N. Parker and Mr Oldfield Thomas, for valuable material; and to these gentlemen, together with Professors Bland Sutton, and D'Arcy W. Thompson, and Drs G. E. Dobson and G. Killian, for their kindly interest in this inquiry.

List of Mammals in which the Intra-narial Epiglottis has been observed post-mortem.

Unless otherwise stated, all were adults.

† Those marked thus are recorded for the first time.

* For references to those marked thus, see this vol. p. 266; for others, see text.

The numbers are those of preparations in the Museum of the Royal College of Surgeons.

a. EUTHERIA.

PRIMATES.

Cebus (? sp.), Stewart, 1518 B.
Cercopithecus sabaeus, Rückert.
Cynocephalus mormon, Waldeyer.
C. sphinx, Rückert.
C. (? sp.), Stewart, 1520.
Homo, fœtus, Sutton.
† *Lemur catta*, Howes.
Pithecus satyrus, juv., Waldeyer.
,, ,, adult, Stewart.
† *Tarsius spectrum*, Howes.

[1] Dr Killian writes me—"You can observe the same situation of the epiglottis in all the older embryos of Mammals."

[2] De Meurron, *Comptes rendus de l'Acad.*, Paris, vol. cii. p. 1403, 1886.

CARNIVORA.

Canis familiaris, Huxley,* Rückert.
C. vulpes, Rückert.
C. (? sp.), Stewart.
Felis domestica, Rückert.
Hyæna striata, Waldeyer.
Lutra vulgaris, Rückert, Waldeyer.
Meles taxus, Rückert.
Mustela foina. M. furo, Rückert.
Nyctereutes procyonides, Garrod.[1]
Phoca anellata, Waldeyer.
P. vitulina, Rückert.
† *P.* (? sp.), Stewart.
Ursus americanus, Waldeyer.
U. labiatus, Waldeyer.
U. maritimus, Waldeyer.

INSECTIVORA.

Erinaceus europæus, Howes,* Rückert.
Talpa europæa, Hunter, Rückert.

CHEIROPTERA.

† *Pteralopex atrata*, Howes.
† *Pteropus edulis*, Howes.
Vespertilio murinus, Robin,[2] Rückert.

RODENTIA.

Castor fiber, Waldeyer.
Cavia cobaya, Rückert.
Hydrochærus capybara, Morgan.*
Lepus cuniculus, Rückert, Howes.*
L. timidus, Rückert, Howes.*
Mus decumanus, Flower.[3]
M. rattus, Rückert.
Sciurus vulgaris, Rückert.

UNGULATA.

Antilocapra americana, Murie.*
Auchenia pacos, Waldeyer.
Bos taurus, Rückert.
Camelus dromedarius, Savi.*
Capra hircus, Waldeyer.
Ceratorhinus sumatrensis, Flower.*
† *Cervus axis*, adult and fœtus Sutton.
C. capreolus, Rückert.
C. dama, Rückert.
C. elaphas, Rückert.
† *Cervulus reevesii*, Stewart.
Dicotyles torquatus, Waldeyer.
Equus caballus, Chauveau, Flower, and various.*
Hippopotamus amphibius,[4] Clarke,* Stewart, 1170 F.
Ovis aries, Rückert.
O. a. (*steatopyga*), Waldeyer.
Phacochærus pallasii, Owen.*
Rhinoceros africanus, Waldeyer.
Sus domestica, fœtus, Killian.
" extra uterine and adult, Owen, Rückert, and others.*
Tapirus indicus, Waldeyer.
† *Tragulus javanicus*, Stewart, 1170 D.

HYRACOIDIA.

† *Hyrax* (? sp.), Howes.
† *H. capensis*, fœtus, Howes.

PROBOSCIDEA.

Elephas indicus, Cuvier,* Stewart, 1170 Mb.
Elephas africanus (?), Mojsisovics.*

SIRENIA.

† *Manatus americanus*, ♂ fœtus, Howes.

CETACEA.

Various. Ray, Cuvier, Flower, and others.*

b. PARATHERIA (EDENTATA).

† *Chlamydophorus truncatus*, Howes.
† *Cholœpus didactylus*, Howes.

[1] *Proc. Zool. Soc.*, 1878, p. 374 (attributed to *Lycdon*, in error, in my former paper).

[2] *Ann. Sci. Nat. Zool.*, ser. 6, vol. xii. art. 2, p. 97, 1881. "Fermant complètement en arrière la cavité buccale, comme chez le Cheval ou l'Éléphant."

[3] "Lectures on the Comparative Anatomy of the Organs of Digestion of the Mammalia," *Med. Times and Gazette*, 1872.

[4] *Cf.* Chapman, *Proc. Acad. Nat. Sci. Philad.*, 1881, p. 130.

Dasypus novemcinctus, Owen,* Rückert.
† *D. sexcinctus*, Stewart.
Myrmecophaga jubata, Flower, 1171 Cb,[1] Waldeyer.
Tolypeutes tricinctus, Garrod.[2]

c. METATHERIA.

Acrobates pygmæus, Poulton.
Macropus melanops, Waldeyer.
M. (? sp.), Rückert.
† *Myrmecobius fasciatus*. Howes.
Petrogale xanthopus, Waldeyer.
† *Phalangista vulpina*, Howes.

d. PROTOTHERIA.

Echidna hystrix, Walker, Stewart, 1171 L.
Ornithorhynchus paradoxus, Rückert.

[1] *Cf.* Sutton, this vol. p. 258.

[2] *Proc. Zool. Soc.*, 1878, p. 227.

ERRATA.

Page 267, line 8 from bottom,	*for*	"completeness"	*read*	"incompleteness."
„ 268, „ 13 from top,	„	"more"	„	"mere."
„ 268, footnote 1,	„	"Hystrix"	„	"Erinaceus."
„ 270, line 9 from bottom,	„	"Dors"	„	"Das."
„ 270, „ 8 from bottom,	„	"epiglotticum"	„	"epiglotticus."

A CASE OF CONGENITAL ABSENCE OF THE TIBIA.

By JOHN SHAW M'LAREN, M.A., M.B., F.R.C.S.E.

THE deformed leg, which is the subject of the following paper, was amputated by Dr Heron Watson just above the condyles of the femur. The patient was a male child two years old. Dr Watson kindly permitted me to dissect the specimen before handing it over to the Museum of the Royal College of Surgeons of Edinburgh. I am indebted to Sir William Turner and to Dr Johnson Symington for kind help in dissecting and describing it.

The limb was well nourished. The upper end of the fibula projected prominently outwards, and lay on a level with the outer condyle of the femur. The inner condyle was dragged down by the contracted inner head of the gastrocnemius, so as to lie opposite a point an inch from the upper end of the fibula. The outer border of the fibula could be felt as a distinct ridge in a straight line from the head to the malleolus externus. Nothing could be felt corresponding to the internal tuberosity of the tibia. The apex of the patella pointed outwards and downwards. There was an entire absence of any prominence corresponding to the internal malleolus. The foot was in a position of extreme talipes equino-varus. Thus the insertion of the tendo Achillis lay behind the fibula more than one inch above the lower end of that bone, while the dorsal surface of the tarsus looked forwards, and lay at right angles to the fibula on the same vertical plane. The upper and outer surface of the cuboid was turned downwards, it and the tip of the external malleolus lying on the same level. The plantar surface of the foot was directed backwards, and even slightly upwards.

On dissecting off the skin and superficial fascia and fat, the deep fascia was found ill-defined. It was attached behind the extensor communis digitorum to the outer edge of the fibula, while it passed inwards to the inner side of or behind the tibialis anticus. Behind that it stretched over the posterior muscles of the leg to be attached again to the outer edge of the fibula,

sending inwards a layer under the sural muscles and another to enclose the peronei.

Musular System—Posterior Aspect.—The gastrocnemius had a normal origin. The inner head was much contracted, so as to draw down the inner condyle of the femur, as above mentioned. The insertion was normal, but the tendo Achillis had drawn up the os calcis as mentioned above. In addition, a narrow but strong ligamentous band passed from the capsule of the knee-joint beside the inner head of the gastrocnemius to the under surface of the belly of that muscle, and seemed to give origin to some of its fibres.

The soleus lay in its usual position, and was well developed, but seemed to arise only from the posterior surface of the head of the fibula. The insertion was normal. The inner edge of the muscle was quite free, unattached to any fascia. The plantaris was absent.

The flexor longus digitorum arose from the *anterior* aspect of the head of the fibula, from the fascia covering it, and from a strong membranous band of the deep fascia lying across the limb under the patella; also at its upper end for half an inch its deeper fibres blended with those of a fleshy mass which lay beneath it, and which subsequently proved to be the popliteus. It was inserted by becoming attached to a common tendon in the sole of the foot, to be afterwards described.

The flexor longus hallucis had a normal origin from the fibula alone. Its insertion was into "the common tendon" at a spot where the fibres of the accessorius were united to that tendon.

The tibialis posticus arose with a pointed end from a strong band of membrane, to be afterwards described, a membrane which seemed to be taking the place of the tibia. Its tendon passed through a groove in the internal annular ligament, and was inserted into "the common tendon."

The popliteus had a normal origin from the femur. Some fibres on the anterior aspect arose from the strong band formed by the deep fascia which passed across in front of the knee-joint, and which gave origin to some of the fibres of the tibialis anticus. The insertion was peculiar. Some fibres on the anterior aspect blended with the adjacent fibres of the tibialis

anticus, which, owing to the absence of the tibia, lay over them. Others attached themselves both to the anterior and posterior surfaces of a membrane which represented the interosseous membrane. A third set of fibres attached themselves, as might have been expected, to the strong tendinous band which was mentioned as taking the place of the tibia.

Anterior Aspect.—The extensor communis digitorum arose normally, except that there was nothing corresponding to an origin from the interosseous membrane or tibia. The insertion was into the three outer toes only.

The tibialis anticus arose from the fibula in connection with the extensor proprius hallucis, and ended in a tendon which joined "the common tendon" by one slip, and attached itself to the inner surface of the internal cuneiform bone by a second.

The extensor proprius hallucis arose in common with the last muscle to a normal extent from the fibula. It passed through a distinct compartment in the annular ligament, and was inserted in the following way:—One tendon was attached to the base of the distal phalanx of the great toe; a second tendon passed off from the first and divided into two, an inner and an outer. The *inner* took the place of the slip from the extensor brevis digitorum (which slip was wanting), and, dividing, was attached to each side of the base of the first phalanx of the hallux. The *outer* slip joined the tendon of the extensor brevis going to the second toe, thus taking the place of the absent slip of the extensor communis, which I mentioned supplied tendons only to the outer three toes. Thus the main tendon of the extensor proprius hallucis supplied the place of the usual slip from the extensor brevis digitorum to the first toe, and of the usual slip from the extensor communis to the second toe. The peroneus tertius was larger than normal.

External Aspect.—The peroneus longus was normal in its origin and insertion. The tendon, after leaving the cuboid, gave off a strong slip from which arose some fibres of the abductor minimi digiti and of the two outer interossei (*i.e.*, the third plantar and fourth dorsal).

The peroneus brevis had a normal origin and insertion, but gave off a tendon which passed alongside that of the peroneus

longus till it reached the external annular ligament, where its fibre spread out and distinctly joined those of the ligament.

Muscles of the Foot.—The extensor brevis digitorum was normal in origin. The insertion took place by only three tendons which were attached to the second, third, and fourth toes, the great toe being omitted. Its tendon to that toe was replaced by a slip from the extensor proprius hallucis.

The abductor hallucis was absent. The adductor hallucis, the flexor brevis hallucis, and the abductor minimi digiti were normal.

The flexor brevis digitorum arose by two heads, viz., from the under surface of the os calcis and from the internal annular ligament. It divided into three instead of four tendons, the fifth toe being omitted. The flexor brevis minimi digiti was normal. The interossei were normal except for the additional origin of the outer two mentioned above.

The accessorius was well developed. The origin was normal, and it attached itself to "the common tendon."

The common tendon was formed under the arch of the foot by the union in a web-like manner of

(*a*) the secondary slip mentioned as coming from the extensor proprius hallucis;
(*b*) the tibialis anticus, which formed the main part of the plantar aspect of the web;
(*c*) the tibialis posticus;
(*d*) the flexor longus hallucis;
(*e*) and the accessorius.

The common tendon thus formed then divided into the four deep flexor tendons of the four outer toes to which they were attached. The lumbricales arose from these as usual.

The strong membranous band which was mentioned as giving attachment to some fibres of the tibialis posticus and popliteus was connected above with the strong fascia lying below the apex of the patella. It passed straight downwards to become blended with a disc of fibro-cartilage lying between the inner side of the fibula and a small part of the head of the astragalus. This band seemed to represent the tibia. The muscles mentioned above were attached to it, a membrane corresponding to the interosseous membrane stretched between it and the fibula for about

the lower half of its extent, and a branch from the anterior tibial artery pierced it at a point corresponding to the position of the normal nutrient artery of the tibia.

The main nerves and vessels were normal.

Region of the Knee-Joint.—The tendons of the sartorius, gracilis, and semi-tendinosus seemed to be attached to the inner side of the capsule of the knee-joint. The capsule was thickened at a part corresponding to the patellar tendon, and blended below with the fascia of the limb, with the band corresponding to the tibia, and with a fibrous mass to be afterwards described, which intervened between the femur and the head of the fibula.

The part representing the trochlear surface of the femur extended higher on the outer than on the inner side, was slightly concave from side to side, and convex from above down. Below it was continuous with the two condyles, which were defective behind, the inter-condyloid notch being rudimentary. The surface of the femur articulated with the patella which was cartilaginous, concave from above down, and surrounded by fat covered with synovial membrane. The femur was found not to articulate directly with the fibula. The upper extremity of the fibula presented towards its anterior portion a facet about a quarter of an inch in diameter, which was separated from the external condyle of the femur by a mass of dense fibrous tissue.

Ankle-Joint.—This joint was formed by the lower end of the fibula and the astragalus. The articular surface of the fibula looked downwards and inwards, and was concave, corresponding to a convexity on the astragalus.

Astragalo-Scaphoid Joint.—This was found to be a small diarthrodial joint, without any evident communication with the articulation between the astragalus and os calcis.

The *calcaneo-cuboid joint* was about twice the size of the astragalo-scaphoid, but natural in shape.

Calcaneo-Astragaloid Joints.—There was very little movement in these joints, which consisted of a small articulation corresponding to the posterior calcaneo-astragaloid joint, and a second between what seemed to represent the sustentaculum tali of the calcaneum and the corresponding surface of the astragalus.

The astragalus had lost its characteristic shape, all trace being

absent of a division into body, head, and neck. It had, in fact, a cylindrical shape. Its larger extremity, directed outwards and upwards, articulated with the fibula, and the smaller with the scaphoid. The anterior part of the tarsus seemed to be normal.

Dr James K. Young, of Philadelphia, has studied the literature of this rare deformity. He mentions (*Internat. Jour. Med. Sci.*, Feb. 1888) twelve cases, to which may be added Dr Craig's case (*Jour. Anat. and Physiol.*, April 1878), in which the tibia terminated in a sharp point almost immediately below the knee-joint. Of these, seven were cases of complete absence of the bone, to which may be added my own; the remainder resembled Dr Craig's, the upper end of the tibia being present. I have not been able to obtain records of all these, but of those I have seen much the most detailed account is to be found in Dr Craig's paper, in which the anatomical description was written by Dr Symington. A study of these accounts suggests some interesting points of comparison.

Femur.—In Billroth's case the condyles of the femur were normal, though the tibia was entirely wanting, and the fibula entered into the joint. Parker says the lower end of the femur was less expanded than usual, while in one of Albert's cases it was "rounded." In my case the condyles were defective posteriorly. In Pauly's case the external condyle was normal in front, but presented an enlarged articular surface outwards, backwards, and upwards for the fibula to glide over. But the most remarkable condition was found in Ehrlich's case of bilateral absence. "Attached to the inner side" of each femur, and projecting "backwards," there was an outgrowth of bone. This projection "was shaped like a cone, with the base flattened from before backwards, and with the apex swelled and rounded." There were no condyles, the lower end of the femur was rounded, and, though feebly developed, it was larger than one single condyle. The projection is not described as entering into the articulation, but corresponded so far to the absent tibia that it gave insertion to the sartorius, gracilis, semi-tendinosus, semi-membranosus and popliteus.

Patella.—In one of Albert's cases the patella was elliptical and small, in mine it was concave from above down, while Billroth describes it as having a process which projected downwards

and inwards, and which, he thought, represented the tibia. In two cases, Parker's and Ehrlich's, the patella was absent.

Fibula.—In some cases this bone was thicker than normal. In one of Albert's cases the head did not articulate with the femur, while in another it did, lying in the inter-condyloid fossa. In my case the fibula did not articulate directly with the femur, a mass of fibrous tissue intervening between the articular surfaces. Billroth mentions that the fibula entered into the knee-joint, but does not describe the articulation. In one of Ehrlich's cases the fibula and femur articulated, a "meniscus" intervening. The lower end of the fibula in Pauly's case entered into an articulation with the calcaneum, separate from the joint between the fibula and the astragalus. Ehrlich describes the ankle-joint as composed of fibula, astragalus, and calcaneum. In Dr Craig's case, and in mine, it was composed of the fibula and astragalus only.

Tarsal Bones.—Billroth describes them as normal in his case —a statement that is difficult to understand, considering the absence of the internal malleolus. The astragalus was much altered in shape in Pauly's case and in mine, in both of which it resembled a cylinder. In Pauly's case it did not articulate with the calcaneum.

Muscles.—The same variations in abnormality are shown here. Two muscles, the flexor longus hallucis and the tibialis anticus, were absent in Billroth's case; and the same number, the flexor longus hallucis and the flexor longus digitorum, were wanting in a case of Ehrlich's. Billroth mentions that the tibialis posticus and the flexor longus digitorum arose from the fascia alone. In my case the latter had an attachment to the head of the fibula, while the tibialis posticus arose from the band representing the tibia. The extra slip, which I describe as coming from the peroneus brevis, is not mentioned elsewhere, as far as I know; and the curious arrangement of the common tendon under the sole of the foot was present only in Craig's and my own cases.

The representation of the absent tibia by the membranous band I have described I do not find mentioned in any other case.

These variations are not easily explained. It would have been natural to expect that, in all those cases in which the

absence of the tibia was not complete, the fibula would have remained excluded from the knee-joint; but that is not the case, and the "rational" position that the fibula took up in one of Albert's cases, implanting itself, as it were, in the femur, so as to be more in a straight line with it, was not assumed in any other case. Again, the absence of any membranous band to indicate the tibia except in one case is remarkable; and equally so is the fact that the bone seems to have been represented in one case by a large projection from the femur outside the knee-joint, and in another by a minute process from the patella within the joint. It is curious to observe, in fact, how "capricious," if I may use the term, are the results which follow from the same fundamental abnormality.

OBSERVATIONS UPON THE MAMMALIAN PHARYNX, WITH ESPECIAL REFERENCE TO THE EPIGLOTTIS.[1] By R. L. Bowles, M.D., F.R.C.P. Lond., *Consulting Physician, Folkestone Hospital.*

The following communication embodies some notes and experimental observations incident upon my investigations upon stertor in animals. The figures which I give will be found to illustrate, in part, facts long recorded; but, as no good drawings of so familiar an object as the Pig's epiglottis have hitherto been published, I supply the want, in the hope that the figures proffered may be of service to workers in general.

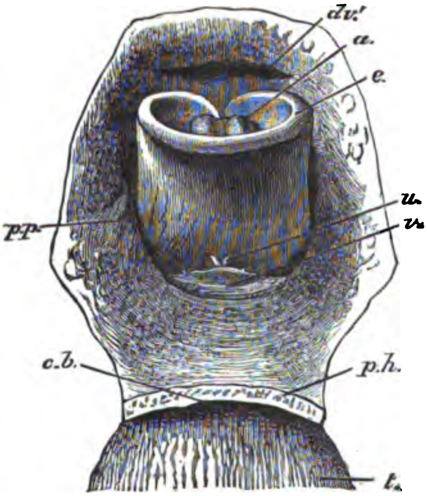


Fig. 1.—Narial pharynx of eighteen-months' Pig, with epiglottis *in situ;* front view, nat. size. *a*, arytænoid; *c.b.*, buccal cavity; *d.v'.*, orifice of diverticulum retro-pharyngeum; *e.*, epiglottis; *p.h.*, cut edge of junction between hard and soft palates; *p.p.*, posterior pillar of soft palate; *t.*, tongue; *u.*, uvula; *v.*, velum.

Comparative anatomists have long ago shown[2] that the characters and relationships of the velum palatinum and epi-

[1] Read before the Anatomical Society of Great Britain and Ireland, March 1889.

[2] See papers by Howes, this vol. p. 263, &c.

glottis are, in many quadrupedal mammals, widely different from those of the human subject. Youatt, writing of the Horse, says[1] the velum forms a perfect division between the mouth and nose, so that although it yields and permits the food to pass under it, in order to enter the pharynx, it prevents the return of the food, and the Horse, except in the convulsive spasms of death, breathes and vomits only through the nose. The epiglottis of the adult Pig is well known to lie, like that of the Horse, above the velum (*e*, figs. 1 and 2), and observation upon the living animal shows that normal respiration is carried on exclusively through the nose. On dissection of the pharynxes

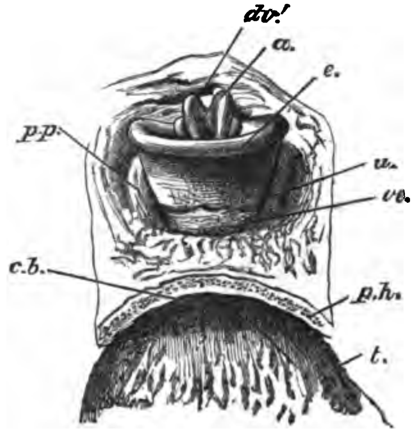


FIG. 2.—Narial pharynx of six-months' Pig, with epiglottis *in situ;* front view, nat. size. References as for fig. 1.

of the adult Horse and Pig a fundamental similarity in disposition of the parts is to be observed.[2] The free border of the velum (which, in the last named animal, bears an insignificant and vestigial uvula, *u*, fig. 1) lies flat upon the tongue, and embraces the upper surface of the same at the root of the epiglottis, in such a manner as to cut off all communication between the mouth and pharynx, except during deglutition. The enormous epiglottis is backwardly extended so as to almost sur-

[1] *The Horse*, London (Gabriel's revision), 1863, p. 213.

[2] Most of the dissections upon which my observations are based were made as follows:—The head was separated from the trunk by cutting through the occipito-atlantal joint, care being taken that the parts about the pharynx were undisturbed, raphé being then divided along the middle line. In Pigs it was found desirable to saw away the occiput before dividing the raphé.

round the aditus laryngis. It stands high up above the level of the arytænoids, and its free border is curled over antero-laterally, whereby its actual apex comes to look downwards and forwards (*cf.* fig.).

An essentially similar condition of the parts is seen in the six-months' Pig (fig. 2), except that the epiglottis is, in it, relatively shorter than in the adult, whereby the arytænoids, *a*, are more fully exposed. The arrangement of the parts is such as would tend to prevent the liquid food, upon which the animal, up to this period, almost entirely lives, from either regurgitating into the nostrils or welling over into the larynx. In front of the palate the mucous membrane at the base of the tongue lies in large loose folds, such as would permit of a great distension of that portion of the buccal cavity during the passage of food; and the parts generally are, in fact, so disposed and modified as to ensure the transmission of the food along the sinus pyriformis, round the epiglottis, into the œsophagus.

The velum palatinum is powerfully developed, and it completely encircles the epiglottis and larynx, forming, at the upper extremity of the œsophagus, a strong sphincter-like band. Immediately behind this there opens a pouch of considerable size (*dv'*, figs. 1 and 9). Chauveau speaks of it[1] as lying "immediately above the glottis, between the thyro- and crico-pharyngeal muscles." It extends back for some distance (*dv''*, fig. 9), and would appear to represent the *diverticulum retropharyngeum* of authors.[2] Concerning its function I have nothing to communicate.

Rückert has recorded the intra-narial condition of the epiglottis in the Sheep (*cf.* Howes, this volume). I find, however, that the same varies in position with animals resting in different positions, and that ordinarily the soft palate does not reach the tongue, while the epiglottis is situated anteriorly to, and (when the animal is prone) at a lower level than, the velum.

Chauveau asserts[3] that in Ruminants there is no arytæno-epiglottidean ligament. I find, however, in an analogous posi-

[1] *Comp. Anat. of Domestic Animals*, Fleming's translation, 1873, p. 376.

[2] Albrecht has suggested that it may be a vestigial homologue of the piscine urine-bladder. *Cf.* Wiedersheim, *Bau des Menschen*, Freiburg, 1887, p. 85.

[3] *Loc. cit.*, p. 462.

tion, a couple of free folds of mucous membrane (*f*, figs. 3 and 4). These structures are, in life, remarkably loose and elastic; they run from the lateral edges of the epiglottis along the outer sides of the arytænoids to the bases of the same, and I conceive of them as functional in protecting the larynx during the regurgitation of food in rumination.

Turning now to the human subject we find that, in the adult, the velum does not reach the tongue. In addition to its function in alimentation, the former is here an important accessory

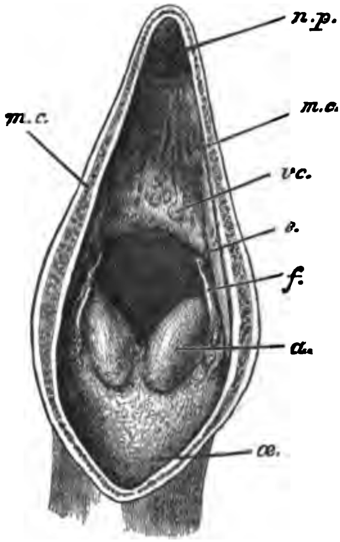


FIG. 3.—The larynx and narial pharynx in the adult Sheep, seen from behind; the constrictors of the pharynx having been divided down the raphé. References as for figs. 1 and 2. *f.*, mucous fold; *m.c.*, constrictor pharyngei muscles, cut edges of; *n.p.*, posterior nares; *œ.*, œsophagus.

to respiration and vocalisation; and it hangs, as it were, in mid-air, ready to respond to the most delicate vibrations and other movements.

I have been struck in the course of my work with the fact that (while much has been done with the comparative anatomy of the adult mammalian larynx) but little attention appears to have been paid to variations and differences due to age in any one case. In the course of my researches into the relative positions of the various parts concerned in the production of stertorous

breathing, I was early struck by the different forms of the epiglottis in many of my subjects, and I ultimately found that this organ differs in shape and position in accordance with the age of the child or quadruped under investigation. In the sucking infant it is curled laterally upon itself, being very convex in front and concave behind; while the rima glottidis is situated relatively higher and closer behind the epiglottis than in later life. The glosso-epiglottidean folds are so disposed as to enclose, on either side, a valley, which lies at a lower level than

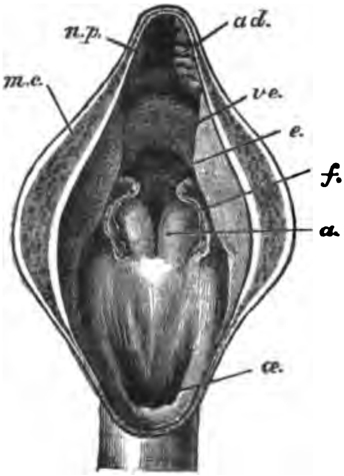


FIG. 4.—The larynx and narial pharynx of an old lamb, seen from behind; nat. size. References as before. *ad.*, adenoid growth.

the glottis; by virtue of the convexity of the front face of the epiglottis, the liquid food of the suckling is directed into the same, being thus prevented from entering the larynx. The uvula, in the few cases which I have examined, fits exactly into the excavated summit of the epiglottis, and the whole condition of the parts suggests an approximation towards that so well known to be realised in the developing marsupial while within the pouch.

As the child ages, the epiglottis expands laterally, and presents an almost plane surface towards the base of the tongue. At the same time the rima glottidis comes to lie, relatively to the free border of the epiglottis, lower down.

I have, from dissections, long been familiar with the fact that at birth, before the child has breathed, not only is there no air-cavity in the chest, but there are no such cavities in the pharynx, mouth, or nares. The various walls and adjacent surfaces are all in close apposition; the base of the tongue lies against the posterior wall of the pharynx, and its upper surface against the palate; the uvula lies behind and against the epiglottis; and

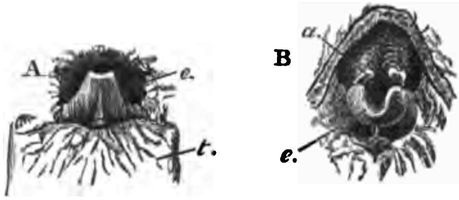
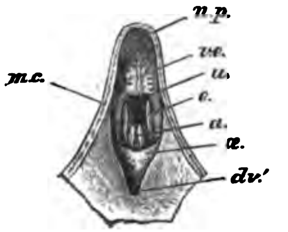
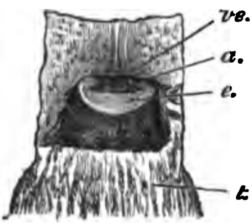


FIG. 5.—The human epiglottis and larynx at twelve months. A, front view; B, top view. References as for previous figures.

the soft walls of the nares, lined with mucus, are all in close contact, and impermeable to air. The first reflex action has for its object the dilatation and opening up of these cavities by forcible separation of their respective walls; but for some months afterwards the palate lies near the upper surface of the tongue, and the uvula is capable of being brought into apposition with the epiglottis.





FIGS. 6 and 7.—6. The narial pharynx of a two-weeks' Pig dissected from behind. 7. The velum and epiglottis of a six-weeks' Pig, front view. Both nat. size. References as for figs. 1–4.

On passing from the human subject to the quadrupedal mammal (Pig), some important and unexpected differences are to be noted, in the correlation of growth and the relationships of the maturating epiglottis and velum palatinum. In the sucking Pig, soon after birth, the epiglottis is to be found in the mouth, below and considerably anterior to the soft palate, while it does

not so far encircle the laryngeal orifice as in later life. The soft palate is less elongated than in the older animal, and the uvula is bifid. The conditions appear to be identical in the fourteen-days' animal (fig. 6), and at this stage the *diverticulum retropharyngeum* (*dv'*) is well developed and proportionately as extensive as in the older Pig.

I have already shown (p. 607, fig. 2) that at six months the epiglottis lies, in this animal, wholly within the narial pharynx, the relationship between the two being exactly in accord with those of the adult. My assistant, Mr Stainer, has introduced his hand into the pharynx of many Pigs of six months and upwards, and has always found the velum to lie anteriorly to (below) the epiglottis and firmly clasping its root. This being so, I was not a little surprised to find that in one animal (said to be five months old) the epiglottis (*e*, fig. 8) lay much more within the buccal cavity than I should have anticipated.

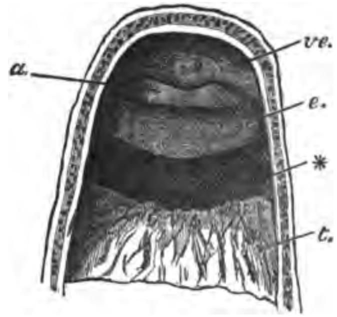


FIG. 8.—The velum and epiglottis of a five-months' Pig; front view, nat. size. References as before.

In the six-months' specimen (fig. 7) the soft palate is seen to have curled in the sides of the epiglottis in such a manner that half of that organ lay in the mouth and half in the narial passage. In the fourteen-weeks' specimen (fig. 9) (the relationships of the parts of which have become somewhat disturbed by repeated manipulation) the relations were much the same, except that a considerably greater portion of the epiglottis was seen to lie in the narial passage. It will be observed that the two last-named animals would appear to be, with respect to general relationships of the parts concerned (as in age), transitional between the earlier and later stages here dealt with, and the facts suggest

the probability that it is within the 5–6 month of extra-uterine life that the Pig's epiglottis finally becomes intra-narial. Further inquiry is requisite for the settlement of the question; but it is clear, from the facts delineated in figs. 1 and 2, that after the sixth month the epiglottis continues to elongate, whereby it ascends the more completely into the narial pharynx.

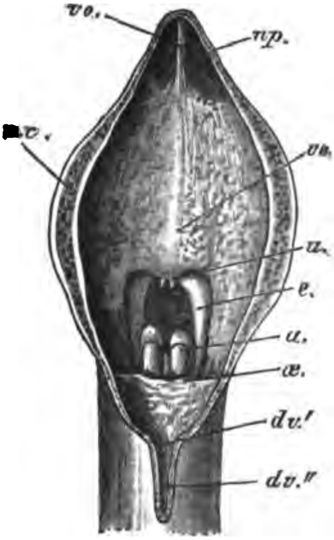


FIG. 9.—The narial pharynx, larynx, and posterior nares of a fourteen-weeks' Pig, seen from behind. The diverticulum retropharyngeum (*dv''*) has been opened up for its whole length. Nat. size. References as for other figs. *vo.*, vomer (posterior edge of nasal septum).

I have examined a series of different forms, with a view of ascertaining how far the facts above recorded for the Pig might be typical of the leading mammalian orders. I am unable to detect between either the Lamb and full-grown Sheep or the Calf and Ox any such remarkable differences as those noted for the Pigs. It might reasonably be expected that in each order a definite type of structure and relationship of the parts under consideration would be discernible. So far as my investigation carries me, this is not the case; for while the arrangement and relations of the palate are, in a series (Horse, Pig, Rabbit, Guinea-pig, and others), similar, the shapes of the epiglottides vary considerably in each member of the same at corresponding ages.

I am able to confirm Howes' observation[1] concerning the intra-narial condition of the Rabbit's epiglottis. When the head is dissected from behind, in the manner which I have adopted, this becomes very striking. It has occurred to me to put the matter to the test of experiment in its bearing upon respiration, and I accordingly stopped up the nostrils of this animal for a short period during life. I found that the creature was, for the time being, quite unable to breathe through its mouth. I have repeated this experiment upon full-grown Pigs with a similar result,[2] and I am inclined to believe that the condition of the epiglottis described by Howes is the normal one for the Rabbit.

In addition to the foregoing, I append some notes of a more general nature, in the hope that they may be of service in the further study of the co-ordinate functions of the great cavities and organs related to the mammalian pharynx.

A Horse cannot breathe or vomit through the mouth, but does it neigh through the mouth or nostrils? A Pig snores or grunts ordinarily through the nose, but who has not heard this animal squeal through its mouth? A Lion ought not (if the anatomy of the pharynx in a six-weeks' specimen in Professor Cleland's series at Glasgow is typical)[3] to breathe, vomit, or emit noises by the mouth; and yet a friend of mine, probably one of the greatest lion-hunters of the age, assures me that Lions open their mouths with their heads low down, and appear to roar through the former. When they attack, however, they throw up their heads and emit sudden yelps like a Dog. Dogs appear

[1] This vol. p. 264.

[2] I saw this experiment performed, for purposes of safety, upon a violent Horse while in Paris during the slippery weather of last year. A large chestnut brougham horse had got his legs entangled between the broken shafts and harness of another horse; in his terror he plunged and kicked most violently, and nothing appeared to be possible to save both animals from destruction, until the coachman got down from his box and grasped the chestnut's nostrils. The animal was at once subdued, and he gradually fell senseless to the ground, remaining there while the harness was cut, and all danger removed. The knowledge of the fact that pressure on the nares will stop the breath in horses is practically utilised in an invention for stopping "bolters" by an arrangement of pads to the nostrils, which can be closed at the will of the rider.

[3] The arch of the palate clipped the root of the epiglottis in front, like that of the Horse or full-grown Pig.

to breathe in ordinary through the nose; they can, however, by volition, breathe as efficiently through the mouth.

Since writing the above, I have elicited the information that Horses, when much excited, neigh through the mouth. I have, moreover, experimented again on the full-grown Pig by stopping up its nostrils for a short time, and have found that although it does not appear to be capable of inspiring by the mouth, it can yell and shriek through it most terribly[1]—shrieking being, of course, the result of an expiratory effort. The same explanation may perhaps apply to the Horse and Lion.

In conclusion, I desire to state that I have been enabled, by dissection, to establish my belief that the cause of death in "cast" or "mislaid" Sheep and Oxen depends upon suffocation from gravitation of the tongue, epiglottis, and other pharyngeal appendages against the posterior wall of the pharynx when the animal is supine. I believe that physiologists have experienced difficulties in conducting certain investigations upon the Rabbit while supine. I have dissected two Rabbits in this position, and find that they would probably have died from the cause alluded to above had they been fixed in supination. I have elsewhere dealt with the cause of stertor in Man[2] and with the fact of its being so common in Swine.[3] I submit, finally, that the great development of the epiglottis in many of the "dumb" animals is opposed to the view which now tends to prevail, that the epiglottis is not primarily protective of the opening of the larynx.

[1] While this paper was passing through the press, I have experimented upon an old boar by corking up his nostrils. I found, in this instance, that the animal could both shriek and breathe through the mouth.

[2] *Trans. Med. and Chirg. Soc.*, vol. xliii. p. 41, 1860; *Proc.* of same, vol. vi. p. 291, 1871; *cf. Lancet*, 1880, p. 971; and Quain's *Dict. of Medicine*, article "Stertor."

[3] Paper on "Stertor in Animals," read before section "Medicine," Brit. Med. Ass., Glasgow meeting, 1888 (not yet published).

THE INFLUENCE OF POSTURE ON THE FORM OF THE ARTICULAR SURFACES OF THE TIBIA AND ASTRAGALUS IN THE DIFFERENT RACES OF MAN AND THE HIGHER APES.[1] By ARTHUR THOMSON, M.A. Oxon., M.B. Edin., *Lecturer on Human Anatomy in the University of Oxford.*

THE tibia presents more variation in length and form than any of the other long bones of the limbs of man.

In regard to the question of length, this view is borne out by the tables of the proportions of the limb bones to the body-height given by Topinard.[2] An analysis of these tables may prove interesting. The greatest proportionate length of the tibia is found among New Caledonians; the average of eight males is 23·8. The smallest tibia is that of a Samoyede, the proportion of which is given at 20·8 to the body-height; the difference between these extremes is 3. In females the difference is even greater. Topinard gives the proportion of the tibia in three female New Caledonians as 24·8, that of a female Aino as 19·9, showing a difference between these extremes of 4·9. (I may here mention that I have not taken the measurement of the tibia as given for the natives of India. The proportion, 28·0 as stated in the table, is evidently a misprint, as is seen by comparing the index given on page 1045.) Similarly, the difference between the extremes of the proportionate lengths of the femur is 2·3 in the males (four Egyptians, 28·3; one Samoyede, 26) and 2·5 in the females (two Tasmanians, 15·6; twenty-five Europeans, 14·3).

In the upper limb the difference in the proportions is relatively less; thus in males the difference in the proportionate length of radius is 1·6 (thirty-two negroes, 15·7; one Samoyede, 14·1), in females the variation is somewhat less. In regard to the humerus, the difference in males is 1·9 (seventy-two Europeans, 20·7; five Chinese, 18·8), in females 1·4.

[1] Read to the Anatomical Society of Great Britain and Ireland, May 30, 1889.

[2] *Eléments d'Anthropologie Generale*, Paris, 1885, pp. 1040–41.

We may thus take it for granted that the length of the tibia is more variable than any of the other long bones.

As regards alterations in form, the flattening of the shaft of the bone to which the term platyknemia is applied, is the variety with which we are most familiar. Busk,[1] Broca,[2] Virchow,[3] Schaaffhausen,[4] Pruner Bey,[5] Khuff,[6] Wyman,[7] Short,[8] Danielli,[9] Topinard,[10] Turner,[11] and many others have referred at length to this matter, and more recently Manouvrier[12] has published a memoir on the subject. As this peculiarity in form of the tibia has some bearing on the subject of the present inquiry, I may be permitted to quote briefly from the conclusions arrived at by that author.

He shows conclusively that the increase in the antero-posterior diameter of the bone takes place behind the inter-osseous ridge, and is due to the largely increased area for the attachment of the tibialis posticus muscle. This increase in bulk of the tibialis posticus he considers as due to an increased activity of its *indirect* action, *i.e.*, from below upward; an action which he maintains is most frequently brought into play in those persons who live in mountainous and difficult countries, or in those whose existence entails the necessity of following the avocation of hunters. In this way he explains its more frequent occurrence in ancient and savage races, and its diminution in frequency under the influence of civilisation. In comparing the platyknemia of man with that which we find in the apes, he draws a distinction and emphasises the fact that in the latter the large development of the tibialis posticus muscle is associated with increased activity in its *direct* mode of action.

[1] *Jour. Ethnol. Soc.*, New Series, 2, 1869–70.
[2] *Bul. de la Soc. d'Anth.*, Paris, 1868.
[3] *Zeit. fur Ethnol.*, Berlin, 1880.
[4] *Archiv fur Anthr.*, vol. xiv., Corresp.-Bl. *der deutschen anthr. Gesellschaft*, Oktober 1882.
[5] *Bul. de la Soc. d'Anth.*, 1886.
[6] *Rev. d'Anth.*, Paris, 1881.
[7] *Report Peabody Museum*, 1878.
[8] *North America of Antiquity.*
[9] *Enciclopedia Medica Italiana*, fasc. ccxxxv., Milano.
[10] *Eléments d'Anthropologie Generale*, Paris, 1885, p. 1020.
[11] *Challenger Reports*, part xlvii., 1886.
[12] *Mem. de la Soc. d'Anth. de Paris*, 2e serie, tome iii. p. 469.

Another change in the form of the tibia is the backward curve of the upper portion of the shaft by which the condyloid surface lies in an oblique plane, when we place the shaft in a vertical position. In my examination of a considerable number of specimens, I was struck with this peculiarity, and was not then aware that attention had been directed to it.

Dr Collignon,[1] in describing some fossil human bones, remarks on this peculiarity of the tibia, and considers that it might be induced by a more habitual state of flexion of the limb, and in consequence he supposes that the gait of these people was less erect than their modern representatives. In support of this view he contrasts the tibiæ he describes with those of the gorilla.

Fraipont[2] noticed a similar formation in the tibiæ of the men of Spy, and in the *Revue d'Anthropologie*[3] further investigates the matter. After a series of experiments he decided that the proper mode of comparison of this form of tibia was to place the bone in such a position that the condyloid surfaces of the tibia lay in the horizontal plane. Under these conditions, when any such curvature as that mentioned above existed, the lower part of the shaft was thrown backward. An examination of the lower articular surface of the femur revealed the fact that the extensor area was not carried so far forward on the anterior surface of the bone as usual, so that from these facts he was led to conclude that the men of Spy, in the erect position, appeared to have the femur and tibia inclined to one another at an angle not so marked as what we see in the anthropoids, but still sufficiently pronounced as to render the difference between Quaternary man and the modern European very characteristic.

From the foregoing, it will be sufficiently clear that in form the tibia undergoes frequent changes, and it will be no less apparent that that change in form is due in most instances at least to the influence of posture.

I was led to undertake the present investigation from the circumstance that in describing a Veddah skeleton my attention was drawn to what I considered an unusual anomaly, *i.e.*, the articulation of the anterior margin of the lower articular surface

[1] "Description des ossements fossiles humains," *Rev. d'Anth.*, Paris, vol. ix., 1880.

[2] *Archiv. de Biologie Gand.*, tome vii., fasc. iii., 1887.

[3] *Rev. d'Anthropologie*, Paris, 3e serie, tome iii. p. 145.

of the tibia with a facet on the neck of the astragalus. This led me to examine very carefully a number of tibiæ in the Oxford collection, with the result that another and equally interesting point was brought under my notice. I extended my inquiries further, and here let me express my indebtedness to Professor Stewart, of the Royal College of Surgeons' Museum, for his great kindness in permitting me to measure the specimens in that museum, and for the facilities he accorded to me for that purpose.

The two points to which I wish to direct your attention are —(1) variations in the form of the external condyloid surface of the tibia; (2) the presence of facets upon the *anterior margin* of the lower articular surface of the tibia and the *neck* of the astragalus respectively.

I. *Variations in the Form of the External Condyloid Surface of the Tibia.*—A reference to most of the English and foreign text-books elicits the fact that the description of the upper articular surface of the tibia is far from satisfactory. Taking one instance only, the surfaces are thus described in Quain:[1]—"On its superior aspect are placed two slightly concave articular surfaces which sustain the femur. These are the condylar surfaces; they are oval in form, the internal being larger than the external, a little more hollowed, and longer from before backwards." Now, such a description, without being inaccurate, is certainly far from complete. Granted that the external condyloid surface is often slightly concave towards the centre, it is a noteworthy fact that the posterior margin is very frequently rounded off; and admitting the occurrence of the slight hollowing of the centre of the surface in the macerated specimen, we will see that this is usually made up for by the increased thickness of the encrusting cartilage over the centre of the area.

The description given by Humphry[2] is more in accordance with fact. "The outer (condyloid surface) is almost flat; it is slightly concave in the transverse direction, but it is slightly convex from before backward, inasmuch as its hinder edge is rounded off to permit the semi-lunar cartilage and the tendon of the popliteus to slide upon it when the joint is bent; and its

[1] *Quain's Anatomy*, 9th ed., vol. i. p. 115.
[2] *Human Skeleton*, p. 527.

anterior edge is flattened to permit the semi-lunar cartilage to pass forward upon it during the slight rotation that accompanies complete extension of the joint. It rises more gradually than the inner articular facet to the spine, and this increases the antero-posterior convexity of its inner part."

Hueter[1] maintains that in the adult the external articular surface retains the convex form found in the new-born child; and Lannelongue,[2] in an account of cases of subluxation of the external semi-lunar cartilage in children of three and eight years old respectively, well describes the external condyloid surface, as follows:—"Denuded of its cartilage, one observes that it is not flat but saddle-shaped from before backwards, and the articular cartilage descends much lower than on the internal tuberosity." Young[3] draws attention to the fact that the vertical antero-posterior section of the external condyle displays a convexity which contrasts markedly with the concavity of the internal condyle. From these observations, it would appear, therefore, that the more common description found in most of the text-books is somewhat misleading.

Whilst, under ordinary circumstances, this convexity, described as above, is but slightly marked, yet if the observations be extended over a considerable number of specimens, instances in which the convexity is more strongly pronounced will not be found wanting; and if, in addition, our examination includes the tibiæ of savage races, the convexity will be found yet more evident.

In order that the results of my inquiry might be in some way systematised, I made my observations in the following way. When dealing with loose specimens I moulded a strip of soft lead across the centre of the external articular surface in the antero-posterior direction; from this I was enabled to take a tracing. All the loose tibiæ were so dealt with, and collecting my results I arranged the tracings into five groups, according to the degree of curvature they displayed. I then numbered these groups from 1 to 5, as shown in the cut, the curves of which are taken direct from the typical tracings. I was thus enabled to

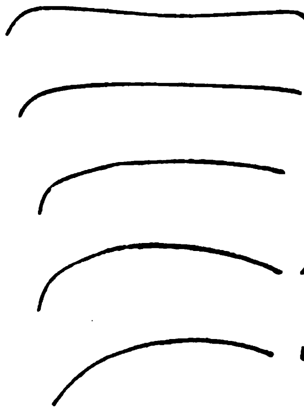
[1] "Das Kniegelenk," &c., *Archiv fur Path. Anat.*, Berlin, 1863, p. 484.

[2] *Bul. et Mem. de la Soc. de Chir.*, Paris, 1879, p. 576.

[3] "Grooves and Lock of Knee-Joint," *Memoirs and Memoranda in Anatomy*, Cleland, Mackay, Young, vol. i. p. 148 (Williams & Norgate, London, 1889).

get a series of curves for comparison, as in dealing with the articulated skeletons I was unable to apply the lead strips to the surface of the bone. I found this method satisfactory enough for all practical purposes.

One hundred and fifty-two skeletons, either partial or complete, were examined; in some cases the upper extremity of the tibia was so diseased or mutilated as to prevent comparison; for this reason the number of instances in which the tibiæ were examined was reduced to one hundred and forty-five. In most cases both tibiæ were inspected, but as the differences between the right and left bones were imperceptible, the contours of the right only have been given in the table; where the right tibia has been wanting, or, from causes above stated, could not be noted, the curve of the left has been substituted. The average curve of the one hundred and forty-five specimens examined is 2·26, that is to say, the convexity of the external condyloid surface is slightly more pronounced than that figured 2 in the type series.



1 2 3 4 5

Further analysis is given in Table No. II., where the different races are grouped geographically. The tibiæ with the flattest condyloid surface are those of the negro, the mean of seven mixed African negroes yields a curve of 1·3; but in this connection a reference to Table No. I., where the records of each individual specimen are given, shows that this flatness of the condyle is associated with marked obliquity of the surface, to which reference will be made subsequently. Of thirty-one mixed Europeans examined, the mean curve is 1·5, and a reference to the type series will show that such a curve intermediate between No. 1, which is almost flat, and No. 2, which is convex, can scarcely be called concave. A further inspection of the Europeans enumerated shows us that of the twenty-nine specimens from which curves were obtained, seventeen had a curvature equal to No. 1, nine to No. 2, two to No. 3, and one to

No. 4. In Table No. II. such analysis has been carried out throughout the entire series of skeletons. The figures in the columns corresponding to the type curves show the number of specimens which displayed curves corresponding to the types enumerated. When the sum of these figures does not correspond with that placed before the description of the skeletons, it is to be understood that the tibiæ of all the specimens have not been accessible for examination. The averages in the column set aside for that purpose have been deduced from the total of the *tibiæ* examined, not from the total of the *skeletons*. Generally speaking they correspond, but there are exceptions.

Closely allied to the European type, but somewhat flatter, is the curve 1·3 of three Eskimo. Three ancient Egyptians yield a somewhat higher average, 1·7.

Four North American Indians, on the other hand, display the greatest convexity, yielding an average curve of 3·2; somewhat less are the six Peruvians, with a mean curve of 3·0. Twenty-five Andamans and three Tasmanians come next with an average of 2·7. Not far behind them come eleven natives of India with a curve of 2·6. Fourteen mixed Australians, four New Caledonians, and two New Hebrideans follow with average curves of 2·5 respectively.

For further particulars the reader is referred to the tables. As will be seen, I have not taken individual specimens as examples in the foregoing remarks, but have noted those averages which have been computed from several specimens.

The series of Andaman tibiæ is remarkable, not only in the variety which their curves possess, but also from the fact that one of the specimens displays the most pronounced convexity I have observed—a curve corresponding to that numbered 5 in the type series.

From these facts it is sufficiently apparent that there are pronounced differences in the form of the contours of the external condyloid surface of the tibia. It is evident that we have the minimum of convexity in the European, whilst in North American Indians, Peruvians, Andamans, natives of India, Australians, New Caledonians, and New Hebrideans we have the convexity most pronounced. The African negroes are remarkable in having the condyloid surface flatter than the European.

How are we to explain these facts? A reference to the

physiology of the knee-joint may perhaps assist us. The external semi-lunar cartilage of the joint differs in regard to its attachments from the internal cartilage in being more loosely connected and possessing a wider range of movement. To facilitate this movement the external condyloid surface of the tibia is convex, the posterior border is especially rounded off. Thus, the external semi-lunar cartilage is permitted to move backward and forward more freely. This backward and forward movement of the cartilage takes place in flexion and extension, coincident with a certain amount of rotation. In the position known as squatting, the legs are flexed upon the thighs, and the thighs on the trunk; the heels are generally some distance apart, and the toes are turned outward.[1] In this posture the back of the thighs rests upon the calf, and the knee-joint is in a state of extreme flexion, associated with a certain degree of rotation of the leg upon the thigh. Now, this is just the position in which we find the external semi-lunar cartilage drawn downward and backward, and I have little doubt but that an increase in the convexity of the condylar surface considerably facilitates this movement. There are then grounds for believing that varying degrees of convexity of the tibial external articular surface indicate pretty precisely the habitual use, to a greater or less extent, of the limb in the flexed position. We find the articular surface flattest in those who do not as a rule make use of this position, most pronounced in those races in which it is the customary mode of resting. The African negroes appear to disagree with this statement; but when the fact is remembered that, in most of these with a flat condyloid surface the articular area was placed very obliquely, associated with a backward curve of the upper extremity of the shaft of the bone, we may find some solution for the discrepancy. As has been already noted, Collignon[2] has stated his opinion that such a curve of the shaft might be induced by habitual flexion of the limb; and doubtless the arrangement is one which is, to some extent, compensatory, and explains the unusual flatness of the condyloid surface.

[1] The probable influence of the squatting posture in modifying the proportions of the pelvic brim has been referred to by Prof. Turner in his *Challenger Report*, part xlvii., 1886.

[2] *Revue d'Anthropologie*, Paris, vol. ix., 1880.

I should, however, state that my attention was not particularly directed to this point at the time I was actually measuring the bones, and it was only in those cases in which the curve of the shaft was so marked as to at once attract attention that the condition was noted as seen in the tables. Had I been aware of the possible importance of this form of tibia in this connection, I might possibly have obtained further evidence in confirmation of the view quoted above.

II. The second part of this inquiry relates to the *presence of facets on the anterior margin of the lower articular surface of the tibia and the neck of the astragalus.*—I have been unable to find any record of such a condition. Taking up the examination of the tibial facet in the first instance, the anterior margin of the lower articular surface on a European tibia will, in all probability, be found sharp, well defined, and unbroken in its continuity. If, on the other hand, we examine the same region in the tibia of an Australian or an Andaman, we can usually notice a facet, more or less distinct, placed on the anterior aspect of the margin near the fibular side, and encroaching on the margin in such a way as to become directly continuous with the surface which articulates with the upper surface of the body of the astragalus. If, now, the astragalus belonging to the same specimen be examined, it will be found that the neck of that bone accurately fits into this facet in extreme dorsiflexion of the foot, and that not unfrequently the neck of the astragalus is provided with a corresponding facet. In regard to the tibial facet, there are many differences in form and extent. In some cases the presence of such a facet is only indicated by an eversion or lipping of the anterior margin of the inferior articular surface; in other instances, this eversion of the margin is associated with a hollowing of the bone around it, the surface of which is smooth, but can hardly be regarded as articular. In these cases we not unfrequently find that there is a tubercular ridge on the neck of the astragalus, the surface of which is smooth, which, in extreme flexion of the foot, fits into this hollow, the surfaces of the bone being in contact. In many specimens, however, the facet is well marked and defined, and varies only in size and form.

Turning now to Table No. II., it will be seen that the specimens have been arranged according, *first,* to those which have

facets in the tibia; *second*, those in which the presence of a facet is doubtful; *third*, those in which there is no facet. In thirty Europeans examined this facet was only found in two instances, in four cases its presence was doubtful, and in twenty-four specimens there was an entire absence of any such facet. Turning now to the Australians, we find the opposite extreme. Thus, in fourteen specimens of that race examined, in no instance was the tibia found without an indication of a facet; in three examples the facet was noted as doubtful; in the eleven remaining specimens the facets were distinct, and more or less clearly defined. Twenty-five Andamans were inspected, and here again no bone was found without some indication of a facet; in five cases the facet is marked doubtful; in eighteen individuals its presence is evident. Similarly, in eleven natives of India the facet is present in six instances, in no case is it doubtful, and in four specimens there is no indication of it. In four Polynesians the facet occurs three times. Reference must be made to Table II. for further information. From what has been stated, however, it will appear that this facetting of the tibia is, in a marked degree, associated with extreme convexity of the external condyloid surface of the tibia. In those races in which we find that convexity most pronounced, we find the occurrence of this facet most frequent, and the coincidence of these features is no doubt due to a similar cause. In the squatting position already described, the ankle-joints are in a state of extreme flexion, *i.e.*, the dorsal surface of the foot is approximated to the anterior aspect of the leg. Now, under ordinary circumstances, the locking of the joint in this position is effected by the wedge-shaped form of the superior articular surface of the astragalus being driven in between the tibia and fibula; but in such cases, where this position of extreme flexion is habitually maintained for long periods, it would appear that the locking of the joint takes place, not in the manner ordinarily described, but by an actual contact of the neck of the astragalus with the anterior border of the lower portion of the tibia. Such an explanation appears to accord well with the facts stated in the tables.

In regard to the facet upon the neck of the astragalus, its presence is, of course, complementary to the facet on the tibia. There is, however, a tendency for it to be less well marked than

on the tibia; as in that bone, we have all transitions in the development of a facet on the neck of the astragalus. Between the condition in which the neck is rough and non-articular, and that in which there is a well-marked facet, the contrast is most marked, but in the intermediate forms the difference is not so evident. The first indication of such a change is a smoothing of the bone along the outer half or third of the upper part of the neck, in such cases the neck is in contact with the anterior margin of the tibia in extreme flexion. The next stage may be described as that in which the articular surface on the superior aspect of the body of the bone becomes insensibly fused with this smooth area, which is now presumably articular. A further advance is seen in those cases where the articular area on the neck of the bone is now clearly defined by a well-marked margin from the non-articular part of the neck; differences in the form and extent of this facet may be noted. Another variety I have observed, and to which I have already drawn attention, is that condition in which we find a tubercular ridge extending across the neck obliquely from the outer towards the inner side of the neck, just behind and more or less parallel to the margin of the scaphoid articular surface. The upper surface of this ridge is usually smooth, and fits into a hollow on the inferior margin of the tibia, such as I have already described, and rests upon it. A feature with which I was struck in the examination of the numerous astragali I handled, was the great variation of the length of the neck of the bone in different specimens. Unfortunately, I took no means to record these differences, but it may prove an interesting field for future inquiry. Unfortunately, in some instances the astragali are wanting, but as a rule the bones corresponding to the tibiæ have been examined. Where the bones are absent the fact is recorded in Table I. by a blank space; when present, and having no facet, a dash is substituted; where a facet is present that fact is stated. Twenty-five European specimens were examined, and of that number twenty-four were without facets, whilst in one only was the facet present. In eleven Australian specimens, those with facets numbered seven; those in which the facet was doubtful, or confined merely to a smoothness of the outer border of the upper surface of the neck, were four in number. In *no* specimen examined was the neck rough and

free from the influence of pressure. In twenty-four Andaman specimens, twelve had facets, seven were doubtful, and five showed no indication of such a condition. Without entering into fuller detail, for which purpose Table II. may be consulted, it appears that the presence of these facets has a distinct relation to the tibial facets, already described, with this difference, as has been already stated, that the tendency is for the facets on the astragalus to be less clearly defined than those on the tibia. I need not here dwell on the cause, an explanation has been already offered in connection with the appearance of these facets on the tibia. It would afford an interesting proof of the conclusions above advanced if such arrangement of facets could be demonstrated in the case of those individuals whose occupation leads them habitually to resort to this position. Miners, while at work, constantly assume a position closely allied to that already described, and I have frequently noticed in mining villages the men seated in this position by the roadside taking their evening smoke after the day's work is done. If, as I am inclined to believe, these alterations in the form of the articular surfaces of the tibia are due to the influence of posture, we should find a confirmation of the fact in such individuals as I have mentioned. Unfortunately, I have had no opportunity of examining such subjects, but it would prove interesting if others with better facilities than I possess would inquire into the matter. It is just possible that the use of strong boots does afford some support to the ankle, and hence we might not find the condition so well marked as in those whose feet are unshod. This fact, however, would not exercise any influence over the knee-joint, and in such individuals we would expect to find a more pronounced convexity of the external condyloid surface than what we ordinarily meet with in Europeans.

The only Neolithic skeleton I have had an opportunity of examining is that known as the Cissbury skeleton in the Oxford Museum. In this specimen the condyloid convexity is pronounced, and corresponds to No. 3 of the type series, and the facets on the tibia and astragalus are well marked and clearly defined—in this respect presenting a marked contrast to the modern European type, and closely resembling that found in lower races at the present day.[1]

[1] Since the above was in type, I have received from Professor Boyd Dawkins

My next object was to ascertain whether this special form of tibia was in any way related to the occurrence of platyknemia. With this intention I made a number of measurements; these, I admit, are far from complete, but I had not an opportunity of noting all the specimens. I have given what measurements I took in the two tables; they may prove interesting for comparison. I took the measurements in the antero-posterior and transverse diameters, according to Broca's[1] method, at the level of the nutrient foramen, but after the experience I have had, I would be inclined in future to adopt the plan recommended by Busk.[2] He took the measurements on a level with the point of convergence of the popliteal line with the internal border. My reason for this preference is, that I frequently found very considerable variation in the level at which the nutrient foramen pierced the bone; and hence the measurements taken did not convey a fair idea of the relative flattening of the bones. In the first column of Table No. II. the average platyknemic index of the specimens examined is given. The number of specimens of which the index is the mean is noted by the small figures placed before the index. In the next columns the extremes of flattening and width in each series are given. The index of platyknemia is obtained by the formula—

$$\frac{\text{Transverse diameter} \times 100}{\text{Antero-posterior diameter}}.$$

When the index falls below 55, then the flattening is pronounced; when the index ranges between that and 69, the compression of the shaft is slight; above 70, the form of the bone is triangular.

It is not my intention to compare the results obtained with

the following information concerning the presence of inferior articular facets on the tibiæ in his possession belonging to the Neolithic and Bronze Ages.

Neolithic Age.

Tibia from Cefn Tomb.—Platyknemic—Facet present.
" " —Platyknemic—Facet present.
" " —Non-Platyknemic—No Facet.
Tibia from Cadz Perthi.
Chwareu.—Platyknemic—No Facet

Bronze Age.

Tibia from Cave Gop.
Denbighshire.—Platyknemic—Facet present.
" —Platyknemic—Facet present.

[1] *Bull. de la Soc. d'Anth.*, Paris, 1868. [2] *Jour. Ethnol. Soc.*, London, 1870.

those of other investigators. I shall content myself with the relation which these results bear to the matter under consideration.

The platyknemic index of twenty-one Europeans is 73·7; the curvature of external tibial condyle is 1·5; and out of thirty specimens, facets on the tibiæ only occur twice, and once on the astragalus.

In fourteen Australians the platyknemic index is 64·1, the tibial convexity equals 2·5, and the inferior tibial facet occurs distinctly eleven times, and three times doubtfully. In seven instances the astragali bear facets; in other four examples these facets are not very distinct. Similarly twenty-five Andamans yield an index of 66·3; a curvature of 2·7; eighteen distinct and five doubtful tibial facet; twelve distinct and seven doubtful instances of facet on the astragalus; and five specimens in which there is no facet on the neck of that bone.

The most platyknemic of all the specimens examined are the three Tasmanians, whose index is only 60·3; they have a high curvature, 2·7; and tibial and astragaloid facets.

From these examples, taken from Table No. II., it would appear that in the races where the index is comparatively high, we have less tibial convexity and fewer inferior tibial facets; whereas, where the index is lower, as in the Australian, Andaman, and Tasmanian, we have these features most strongly pronounced. The association of these peculiarities do not appear to have any direct relation to each other. Thus, if Table No. I. be examined, it will be found that examples are not wanting where well-marked triangular tibiæ display pronounced convexity and inferior facets (Andaman, No. 1216, and Peruvians, Nos. 10, 130, 1014); on the other hand, tibiæ with pronounced flattening sometimes do not exhibit these characters (Fuegian, No. 1025, and Gilbert Islander).

The occurrence of these conditions together in the same individual is rather due to a coincidence than to any direct association, and the fact that the tibial convexity and the inferior tibial facets occur most frequently in those races with a low platyknemic index, is due to the fact that it is in these same races that we find the individuals most frequently subjected to the influences which produce this flattening. To this subject I have already referred at the commencement of this paper. There are too few facts to permit of any conclusions being

drawn with regard to the relation of the conditions herein described to that mentioned by Collignon.[1] It is only exceptionally that I have noted this condition in Table I., by the addition of the word "oblique" after the figure indicating the condyloid convexity. I regret this all the more now that I see the possible importance of this backward curvature of the upper part of the shaft. It was only in those instances in which this curvature was most pronounced that I thought it worth recording. Dealing with the very meagre record of this in Table I., it is seen noted in one European, one Fuegian, one Australian, one New Caledonian, three African negroes, and one Bushman. In the Australian and New Caledonian it is associated with a condyloid convexity below their average. In the negroes, as already remarked, it is combined with a flat condyloid surface. How far this is dependent on the backward curvature of the upper part of the shaft of the tibia, dispensing with the necessary arrangement whereby the external semi-lunar cartilage may glide back more freely in the flexed position, it is difficult to say. The matter is one which requires investigation. The only other example noted is that of a Bushman. Here, again, the condyloid surface is flat, its curvature equal, No. 1, contrasting markedly with those of the other two, whose average is 2·5.

Extending my inquiry into an examination of the corresponding bones in the higher apes, I noted first the strongly-marked and pronounced convexity of the external condyloid surface. This reaches its maximum in the Gorilla, the mean curve of six specimens is indicated by the figure 3·4, corresponding to the type series. The Gibbon, of which one specimen only was examined, came next, with a convexity equal to No. 4 of the type series. Next came seven Chimpanzees, with an average of 3·5; and, closely related, eight Orangs, with a curvature of 3·3. Three Baboons also were noted. They were somewhat flatter on the condyloid surface; their mean corresponds to No. 3 of the type series.

The apes are, therefore, more convex on the external condyloid surface of the tibia than any of the races of men. In no instance is an absolutely flat surface recorded, but specimens are noted with curves equal to Nos. 2, 3, and 4 of the series, so

[1] *Rev. d'Anth.*, Paris, vol. ix., 1880.

that in these examples the difference between them and man is not great.

In regard to the occurrence of the inferior tibial facet, this was found in all five Gorillas examined, and in all the Orangs (eight) and Baboons (three). In six Chimpanzees the facet was only recognised once; in the other five specimens it was remarkable for its absence. In the only Gibbon examined there was no inferior tibial facet.

Similarly, in the astragali of five Gorillas the facet on the neck was distinct in two cases; not so distinct in three specimens. The facet was present and well marked in all the Orangs (eight) and Baboons (three) examined. In five Chimpanzees its presence was only noted once; in the other four it was absent. In one Gibbon examined there was no indication of a facet.

The specimens examined above are those in the collection of the Royal College of Surgeons of England. Some are young, and some are adult specimens. In two young Orangs the specimens were dried with the ligaments still in position, and in each case the dried cartilage could be seen extending forward on the neck of the astragalus, thus leaving no doubt that in these apes at least the smooth surface seen on the neck of the macerated bone is undoubtedly articular.

There can be little doubt that these peculiarities of the knee and ankle in the ape owe their development to the same causes as those which have been offered in explanation of their occurrence in man, though why the inferior tibial facet should be absent five times out of six in the case of the Chimpanzees it is difficult at first to understand.

When seated, the anthropoids do not squat like men; they do not rest the weight of the body on the sole of the foot. In their case, therefore, it is probable that, whilst the cause is the same, *i.e.*, extreme dorsiflexion of the ankle-joint, the production of that flexion is due to a different use of the foot, and is possibly dependent on the free use of the foot in climbing, in which act, no doubt, the weight of the body is for lengthened periods sustained by the foot, with the ankle-joint in an extreme state of flexion. We thus find the tibial and astragaloid facets best developed in the Orangs, which have the reputation of being the most expert climbers of all the anthropoids.

The tibiæ in the specimens examined have comparatively high indices of platyknemia—that is to say, the lateral compression of the shaft of the bone at the level of the nutrient foramen is not pronounced. In the Baboons, in which the upper part of the shaft of the bone is much curved in a backward direction, the degree of curvature of the external condyloid convexity is somewhat less than we meet with in the Chimpanzee, Gorilla, and Orang.

From what has been stated it would appear that these facets and the pronounced condyloid convexity are found alike in the savage races of men and the apes, but that this correspondence in no sense implies that man has received these characters from an ape-like ancestor. In both cases they are due to the same cause—a more habitual use of the limb in the position in which the knee and ankle are forcibly flexed. The condition is one which may probably be acquired, and the higher races of men are characterised by the absence of these conditions merely because their mode of life does not as a rule necessitate such extreme flexion of the knee and ankle.

Summary.

1. The external condyloid surface of the tibia presents varying degrees of convexity in the different races of man.
2. In the higher races the convexity of this surface is but slight.
3. It is most pronounced in savage races, and probably also will be found characteristic of ancient races and fossil man.
4. This convexity appears to be developed in connection with the more frequent use of the limb with the knee strongly flexed.
5. In all probability the position in which the limb is habitually used with the knee bent is that known as "squatting."
6. As yet, there are insufficient data to form any conclusion as to the relation of this tibial convevity with a backward curve of the upper part of the shaft of the bone. From the few facts stated it would appear that there is reason to suppose that the condyloid convexity is less when the backward curve is present.
7. Facets are occasionally developed on the anterior margin of the inferior articular surface of the tibia, and on the neck of the astragalus, these facets come into contact with each other in extreme flexion of the foot on the leg.
8. These facets are of rare occurrence in the higher races.
9. They are found almost invariably in the savage races.

10. They are probably acquired by the constant use of the limb in the position in which the ankle is forcibly flexed.

11. In the "squatting" position the whole weight of the body is thrown on the foot with the ankle in this position.

12. This position is only exceptionally made use of in the higher races; in the lower races it is a habitual posture.

13. This fact explains the frequent occurrence of these facets in the lower races, and their rarity in the higher.

14. The foregoing conditions do not appear to have any direct relation to the flattening of the shaft of the tibiæ occasionally met with.

15. Platyknemia occurs most frequently in those races the members of which dwell in rough countries, and who have to obtain a subsistence by occupations, *i.e.*, climbing and hunting, which bring more forcibly into play the muscles of the leg, the tibialis posticus in particular.

16. The co-existence of these two peculiarities in the same races is, therefore, only accidental.

17. The apes are characterised by well-marked condyloid convexities.

18. Produced, no doubt, by more constant use of the limb with the knee flexed.

19. The Gorilla and Orang have the inferior tibiæ and astragaloid facets usually well marked. The Chimpanzee does not appear to display this peculiarity so frequently.

20. In the above, the production of these facets would appear to be due to a frequent use of the foot with the ankle firmly flexed.

21. In the apes, in all probability, the limb is most frequently employed with the ankle flexed in the act of climbing.

22. The foregoing peculiarities are common to man and the apes, and are due to the influence of posture.

23. There is nothing to lead us to suppose that these peculiarities are transmitted characters, the bulk of the evidence, on the other hand, goes to prove that they may be acquired.

EXPLANATION OF TABLES.

TABLE I.—When not otherwise stated, the numbers in the first column refer to the Catalogue of the Royal College of Surgeons of England Museum. Those marked (B. D.) belong to the Barnard Davis collection, the catalogue number of which is given. The remaining specimens belong to the Oxford collection, and are so marked. In the column headed "Curvature of External Condyloid Surface of

Tibia," the figures refer to the numbered curves of the type series. In the column headed "Inferior Tibial Facet," a blank implies that the tibiæ were either wanting or mutilated. A *dash* means that *no facet* was present on the bone examined. The term "Bevelled" is employed to indicate a slight lipping of the articular margin, and a note of interrogation after the word facet implies that its presence is somewhat doubtful. An asterisk, on the other hand, implies that the facet is particularly well marked. The same remarks apply to the column set aside for the Astragalus.

TABLE II.—The smaller numbers placed before the average index of platyknemia indicate the number of specimens from which the average index was computed. It may be well to remind the reader that pronounced flattening is indicated by a *low* index of Platyknemia and *vice versa.*

In regard to the column marked "Facet on Tibia doubtful," the figures indicate the number of specimens which in Table I. were marked "Bevelled" or "Facet?" The same applies to the figures in the column marked "Facet on Neck of Astragalus doubtful."

TABLE I.

	Diameters of Tibia.		Index of Platyknemia.	Curvature of External Condyloid Surface of Tibia.	Inferior Tibial Facet.	Facet on Neck of Astragalus.
	Transverse.	Ant. post.				
European(English), 67	23	37	62·2	1	—	—
„ 68	27	35	77·1	1	—	—
„ 69	30	33	90·9	1	—	—
„ 70	23	32	71·9	1	—	—
„ 70A	18	29	62	2	—	—
„ 75	...	...	...	1	—	—
„ 76	...	...	...	1	—	—
„ O Brien), 223	35	50	70	2	—	—
„ 224	Disea	sed	...	1	—	—
„ 298	...	...	...	2	—	—
„ 318	...	...	...	Mutilated	Facet	
„ 320	...	...	...	1	Mutilated	
„ 338	...	...	...	2	—	—
„ 346	...	...	...	3	Facet	Facet
„ 330A	...	...	...	1 very oblique	—	
Tibiæ in Oxford 1	26	36	72·2	1	Bevelled	—
Collection, 2	22·5	31	72·5	2	—	—
„ 3	24	31	77·4	2	—	—
„ 4	25	34	73·5	Injured	—	—
„ 5	30	34·5	87	1	Bevelled	—
„ 6	26	35·5	75·3	1	Bevelled	
„ 7	21·5	29·5	72·8	4	—	—
„ 8	23	32	71·9	3	—	—
„ 9	26	38	68·4	1	—	—
„ 10	25·5	39	65·3	1	—	—
„ 11	26	32	81·2	1	—	—
„ 12	23·5	33·5	70·1	2	—	—
„ 13	27·5	35	78·5	1	—	
„ 14	20	29	69	2	Bevelled	—
„ 15	28	35	80	1	—	—
Neolithic (Oxford),	20	34	58·8	3	Facet	Facet*
Antiparos (R. C. S.), 531	...	...	...	2	—	
Lapps, . . 554	...	...	...	2	Bevelled	Facet
„ . . 554A	20	31	64·5	2	Facet	Facet
„ . . 554B	21·5	29·5	72·8	2	—	—

TABLE I.—*continued.*

		Diameters of Tibia.		Index of Platyknemia.	Curvature of External Condyloid Surface of Tibia.	Inferior Tibial Facet.	Facet on Neck of Astragalus.
		Transverse.	Ant. post.				
Lapps,	556	...	...	...	2	——	
,,	557	...	...	...	Mutilated	Facet	
Guanche,	566	...	...	...	2	——	——
,,	569	...	...	...	...		Facet
,,	573	...	...	...	2	——	——
Ancient Egyptian,	583	22	33	66·7	2	——	——
,, ,,	583A	...	...	...	2	Facet small	——
,, ,,	583B	...	...	...	1	——	——
Afghan,	630A	...	...	...	3	Facet	Facet
Panjabi,	631A	...	...	...	3	Facet	Facet
Sikh,	631B	...	...	...	3	Facet	Facet
Sikh (B. Davis),	582	25	34·5	73·5	3	——	——
Punjab,	635	...	...	...	2	Bevelled	——
Orissa,	635B	...	...	...	3	——	——
,,	635C	...	...	...	2	Facet one side only	Facet
Hindoo,	636D	...	...	...	3	Facet	Facet
,,	636E	...	...	...	2	Facet	Facet
Bhutan,	652	...	...	...	3	——	——
Bhutea (B. D.),	797	21	31	67·7	2	——	——
Aino (B. D.),	847	...	...	...	4	Hollowed out	Ridge with smooth surface
Maldive Islands,	674A	...	...	...	2	Facet	Facet
Samoyede,	684	21	30	70	3	Facet	Facet
Chinese,	691A	...	...	...	2	——	——
,, (B. D.),	1017	...	...	...	2	Facet	Facet
Japanese,	711A	Diseased		...	2	——	——
Borneo,	733	...	...	...	2	——	——
Veddah (Oxford),		22	31	71	2	Facet	Facet *
,, (R. C. S.),	680A	21	27	77·7	2	Bevelled	——
,, ,,	680B	20	29	69	2	Facet	Facet
Savage Islands,	757	26	35	74·3	2	Facet	Facet
Java (B. D.),	898	22·5	33	68·1	3	——	——
,, (B. D.),	897	20	31	64·5	3	Bevelled	
Tahitian,	800	20	32·5	61·5	4	Facet	Facet
Gilbert Islands (Oxford),		22	33	67·7	1	——	——
Eskimo,	834	24·5	35	70	2	Facet	Facet
,,	835	21·5	29·5	72·8	1	——	——
,,	836	...	...	...	1	——	——
North American Indian (B. D.),	1239	...	...	...	3	Bevelled	Slight
New Bogota,	889	...	...	...	3	——	
Peruvian,	999	...	...	...	2	——	
,,	1013	22	28	78·5	3-4	Facet	Facet
,,	1014	22	28	78·5	3	Facet	Facet
,, (Mummy),	1014A	...	...	...	3	Facet	Facet
,, (Oxford),	A	21	31	67·7	3	Facet ?	Facet ?
,, (Oxford),	B	16	28	57·1	3	Bevelled	——
Coquimbo,	1015	20	27·5	72·7	3	Facet	
Akawoi Indians, B. Guiana, Oxf.	A	18	27·5	65·4	3	Bevelled ?	
	B	19	28·5	66·6	4	Bevelled	
	C	19	33	57·6	3	Facet	Facet
Tierra del Fuego,	1025	21	36	58·3	1	——	
Ooshooia,	1025B	22	33	66·7	Injured	Bevelled	——
,,	1025C	21·5	38	56·5	2 oblique	Facet ?	Facet ?

TABLE I.—*continued.*

		Diameters of Tibia. Transverse.	Diameters of Tibia. Ant. post.	Index of Platyknemia.	Curvature of External Condyloid Surface of Tibia.	Inferior Tibial Facet.	Facet on Neck of Astragalus.
Ooshooia, .	1025B	18·5	30	61·6	3	Bevelled	
Australians, .	1028	22	38	57·8	2 oblique	Facet *	
,,	0132	26	39	66·6	2	Facet	Facet *
,,	1043	19·5	29	67·2	3–4	Facet *	
,,	1044	21·5	33·5	64·1	3	Facet *	Facet *
,,	1045	21·5	40	53·7	2	Bevelled ?	Facet ?
,,	1066	23	37	62·2	2	Facet	Facet
,,	1068A	26·5	40	66·3	2–3	Facet	Facet
,,	1077A	18·5	33	56	2	Facet *	Facet
,,	1077F	24	38	63·2	2	Bevelled ?	
,,	1088	19·5	28	69·6	3	Hollowed out	Smooth ridge
,, (B. Davis),	1398	19	29	65·5	3	Facet	Facet ?
,, (B. Davis),	1399	22·5	32·5	69·2	3–4	Facet	Facet ?
,, (Oxford),	A	23	33	69·7	2	Facet	Facet
,, (Oxford),	B	23·5	35	67·1	1	Facet	Facet
New Caledonia,	1020A	24	36	66·7	3	Bevelled	
,,	1022	22·5	35	64·3	2 oblique	Bevelled	
,,	1025	18	29	62	3	Facet	
New Hebrides,	1149	26	38	68·4	2	Bevelled	Facet ?
,, (B. D.), .	1438	27	38	71	3	Facet	Facet *
New Caledonia ,, (Oxford),	A	25	39	64·1	2	Facet	Facet *
Loyalty Islands (B. D.), .	1434	22	34	64·7	4	Facet	Facet *
Tasmanian, .	1096	22	38·5	57·1	2	Facet	Facet ?
,,	1097	18	29·5	61	3	Facet	Facet
,, (B. D.),	1406	22	35	62·9	3	Facet	Facet
Papuan, . .	1188	26	39	66·6	2	Facet	Facet ?
,, (Oxford),	A	22	33·5	65·6	2	Injured	
,, (Oxford),	B	16	29	55·1	2	Facet	Facet *
Andaman, .	1203	18	24	75	4	Bevelled	Facet ?
,,	1206	17	28·5	59·6	3	Facet	——
,,	1207	19·5	28·5	68·4	3	Facet	Facet ?
,,	1208	16	27	59·2	4	Injured	——
,,	1209	19·5	30	65	1	Facet *	Facet
,,	1210	21	31	67·7	3	Facet	Facet
,,	1212	16·5	25	66	3	Facet 1 side	Facet 1 side
,,	1213	16	25	64	3	Facet	Facet
,,	1214	19	26	73	1	Facet	Facet
,,	1215	16·5	25	66	2	Bevelled	Facet
,,	1216	18	22	81·3	4	Facet	Facet ?
,,	1216A	20·5	28	73·2	1	Facet ?	——
,,	1218	18	26	69·2	2	Facet *	Facet ?
,,	1217		Dis	eased			
,,	1472	18	28	64·3	4	Facet	Facet
,,	1473	21	29	72·4	3	Facet	Facet
,, (B. Davis),	1474	18·5	27	68·5	3	Bevelled	——
,, (B. Davis),	1476	17	28	60·7	3	Facet *	Facet *
,, (B. Davis),	1479	20	31	64·5	3	Facet *	——
,, (B. Davis),	1480	17·5	28·5	61·4	2	Facet	Facet
,, (Oxford),	A	19·5	30·5	63·9	3	Facet	Facet *
,, (Oxford),	B	16	24	66·6	4–5	Facet	Facet ?
,, (Oxford),	C	17	28	60·7	3	Bevelled	Facet ?
,, (Oxford),	D	17·5	29	60·3	2	Facet	Facet ?
,, (Oxford),	E	20	33	60·6	1	Facet	Facet

TABLE. I.—*continued.*

	Diameters of Tibia.		Index of Platyknemia.	Curvature of External Condyloid Surface of Tibia.	Inferior Tibial Facet.	Facet on Neck of Astragalus.
	Transverse.	Ant. post.				
New Zealand (Oxford), . .	27	36	75	1	Facet	
Africa, Negro Abyssinia, 1219	20	31	64·5	1 oblique	——	——
S. Amer. Slave, 1236		Tibiæ	wanting			Facet ?
Negro, . . 1238	22	31·5	69·8	3	Facet ?	—— ?
W. Africa, . 1249	23·5	30	78·3	1 oblique	——	——
„ . 1250	19	28	67·8	1	Facet	Facet
Abyssinia, . 1257A	22	28	78·5	1	——	——
Balumba (B. D.), 1596	19	33	57·6	1 oblique	Facet	Facet
Bushman, . 1300	22·5	31	72·5	1 oblique	Bevelled	Facet ?
„ . 1301	19	29	65·5	3	Facet	Facet
„ . 1302	18·5	26·5	69·8	2	Bevelled	——
Hottentot (B. D.), 1623	20	30	66·6	2	Facet ?	Facet ?
SIMIIDÆ—						
TROGLODYTES NIGER.						
Adult male, 1	17·5	28·5	61·4	4	——	——
female, 2	17	23	73·9	4	——	——
male, 3	17	27	63	3	Facet small	Facet small
female, 4	14	20	70	4	——	——
„ 5	14	22	63·6	4		
„ 6	16	25	64	3	——	——
Young male, 7	16	24	66·6	3	——	
GORILLA SAVAGII.						
Adult male, 20	21	36	58·3	4	Facet	Facet ?
male, 21	...	...	...	...	...	Tubercular ridge with smooth surface
male, 22	20	31	64·5	5	Facet	Facet
Old female, 23	17	26	65·3	4	Facet	Facet
young, 29	14	22	63·6	4	Facet	Facet ?
female, 24	17	27	63	5	Facet	
SIMIA SATYRUS.						
Adult male, 37	17	22	77·2	3	Facet	Facet *
„ male, 38	17	24	70·8	3	Facet	Facet *
„ male, 40	9	17	53	2	Facet	Facet
female, 40A	14	19·5	71·7	2	Facet	Facet
Nearly adult, 40B	14	18	77·7	5	Facet *	Facet *
male, 38A	17	23	73·9	5	Facet	Facet *
Young female, 47	The cartilage is seen extending forward on the neck of the astragalus. The specimen having been dried.					
young, 51	Dried with ligaments and cartilage still *in situ* neck of astragalus, distinctly articular.					
HYLOBATES SYNDACTYLUS.						
male, 58	9	14·5	62	4	——	——
CERCOPITHECIDÆ						
CYNOCEPHALUS.						
Hamadryas, male, 180	10·5	19·5	53·8	4 oblique	Facet	Facet
Babouin, young male, 184	10·5	17·5	60	3 oblique	Facet	Facet
Leucophæus, male, 197	14	20	70	2 oblique	Facet	Facet *

TABLE II.

	Average Index of Platyknemia.	Maximum of Platyknemia.	Minimum of Platyknemia.	Average Curvature of External Condyle.	Type Series. Curvature No. 1.	Curvature No. 2.	Curvature No. 3.	Curvature No. 4.	Curvature No. 5.	Facet on Inferior Margin of Tibia.	Facet on Tibia doubtful or Margin Bevelled.	No Facet on Inferior Margin of Tibia.	Facet on Neck of Astragalus.	Facet on Neck of Astragalus doubtful.	No Facet on Neck of Astragalus.
EUROPEANS—															
31 Mixed Europeans,	[21] 73·7	62	90·9	1·5	17	9	2	1	...	2	4	24	1	...	24
1 Neolithic,	58·8	...	...	3	...	...	1	...	...	1	...	...	1	...	...
5 Lapps,	[2] 68·6	64·5	72·8	2	...	4	...	...	...	2	1	2	2	...	1
3 Guanche,	..	...	...	2	...	2	...	...	...	...	...	2	1	...	2
NORTH AFRICA—															
3 Ancient Egyptians,	[1] 66·7	...	...	1·7	1	2	...	...	...	1	...	2	...	...	3
ASIA—															
11 Natives of India,	...	...	...	2·6	...	4	7	...	...	6	1	4	6	...	5
1 Aino,	...	...	...	4	...	...	...	1	...	...	1	...	...	1	...
1 Maldive Islander,	...	...	...	2	...	1	...	...	...	1	...	...	1	...	...
1 Samoyede,	70	...	...	3	...	...	1	...	...	1	...	...	1	...	...
2 Chinese,	...	...	...	2	...	2	...	...	...	1	...	1	1	...	1
1 Japanese,	...	...	...	2	...	1	...	...	...	...	...	1	...	...	1
1 Native of Borneo,	...	...	...	2	...	1	...	...	...	...	...	1	...	...	1
3 Veddahs,	[3] 72·5	69	77·7	2	...	3	...	...	...	2	1	...	2	...	1
2 Javanese,	...	64·5	68·1	...	...	...	2	...	...	...	1	1	...	...	1
POLYNESIA—															
4 {1 Savage Islander, 1 Tahitian, 1 Gilbert Islander, 1 Maori,}	[4] 69·3	61·5	75	2	2	1	...	1	...	3	...	1	2	...	1
AMERICA—															
3 Eskimo,	[2] 71·4	70	72·8	1·3	2	1	...	...	...	1	...	2	1	...	2
1 North American Indian,	...	...	...	...	...	...	1	...	...	...	1	...	...	1	...
4 South American Indian,	[3] 63·2	57·6	66·6	3·2	...	...	3	1	...	1	2	1	1	...	...

TABLE II.—*continued.*

	Average Index of Platyknemia.	Maximum of Platyknemia.	Minimum of Platyknemia.	Average Curvature of External Condyle.	Type Series. Curvature No. 1.	Curvature No. 2.	Curvature No. 3.	Curvature No. 4.	Curvature No. 5.	Facet on Inferior Margin of Tibia.	Facet on Tibia doubtful or Margin Bevelled.	No Facet on Inferior Margin of Tibia.	Facet on Neck of Astragalus.	Facet on Neck of Astragalus doubtful.	No Facet on Neck of Astragalus.
AMERICA—*continued.*															
6 Peruvians,	[4] 70·4	57·1	78·5	3	...	1	4	1?	...	3	2	1	3	1	1
1 Chili,	72·7	...	...	...	...	...	1	...	...	1	..	...	...	...	...
4 Fuegians,	[4] 60·7	56·5	66·7	2	1	1	1	...	...	1	2	1	...	1	1
AUSTRALIA—															
14 Mixed Australians,	[14] 64·1	53·7	69·7	2·5	1	7	4	2	...	11	3	...	7	4	...
MELANESIA—															
3 Tasmanians,	[3] 60·3	57·1	62·9	2·7	...	1	2	...	...	3	...	...	2	1	...
4 New Caledonians,	[4] 64·2	62	66·7	2·5	...	2	2	...	...	2	2	...	1	1	...
2 New Hebrides,	[2] 69·7	68·4	71	2·5	...	1	1	...	...	1	1	...	1	1	...
1 Loyalty,	[1] 64·7	...	...	4	...	...	...	1	...	1	...	...	1	...	...
3 Papuans,	[3] 62·4	55·1	66·6	2	...	3	...	...	...	2	...	...	1	1	...
25 Andamans,	[24] 66·3	59·2	81	2·7	4	4	11	4	1	18	5	...	12	7	5
SOUTH AFRICA—															
7 Negroes, mixed,	[6] 69·4	57·6	78·5	1·3	5	...	1	...	...	2	1	3	1	1	4
3 Bushmen,	[3] 69·2	65·5	72·5	2	1	1	1	...	...	1	2	...	1	1	1
1 Hottentot,	66·6	...	...	2	...	1	...	...	...	...	1	...	...	1	...
7 Chimpanzees,	[7] 66	61·4	73·9	3·5'	...	...	3	4	...	1	...	5	1	...	4
6 Gorillas,	[5] 62·9	58·3	65·3	4·4	...	...	...	3	2	5	...	...	2	3	...
8 Orangs,	[6] 70·7	58	77·7	3·3	...	2	2	...	2	8	...	...	8	...	...
1 Gibbon,	[1] 62	...	...	4	...	...	...	1	...	...	...	1	...	...	1
3 Baboons,	[3] 61·2	53·8	70	3	...	1	1	1	...	3	...	...	3	...	...

THE PLACENTATION OF THE *HALICORE DUGONG.*

By Professor Sir WILLIAM TURNER.

(Abstract of a Memoir read to the *Royal Society of Edinburgh*, July 1, 1889.)

THE only observations hitherto recorded on the placentation of the Dugong are by Paul Harting, of Utrecht, in 1878, who examined the fœtal membranes of a fœtus 27·8 cent. long. He stated that the placenta was diffused and non-deciduate.[1]

The gravid uterus described in this communication was presented to the author by C. W. de Vis, Esq., M.A., curator of the Queensland Museum, Brisbane, through Professor Anderson Stuart of the University of Sydney.

The uterus was bicornuate, and contained a single fœtus, 5 feet 4 inches long. The fœtus and its membranes occupied the left cornu, and there was no extension of the membranes into the right cornu.

The chorion was an elongated sac, upwards of 5 feet long from pole to pole.

The placenta formed a zone a little on one side of the equator of the chorion. The zone was 11½ inches broad in its widest part and 6 inches at its narrowest. The rest of the chorion was smooth and free from villi. The villi were closely crowded together in the fœtal placenta. As a rule they were short, though longer ones were interspersed amongst them; they were cylindriform and filamentous in shape, branching seldom and bifurcating near their free ends.

The allantois was very extensive, and reached to the opposite poles of the chorion. Connected to the outer wall of its sac, formed by the endochorion, were a number of plate-like allantoic bodies.

The amnion was very capacious, and was completely surrounded by the allantois, except for a limited area in the region of the placenta. No amniotic corpuscles projected from its inner surface.

The uterine mucous membrane had a zone which formed the

[1] See abstract of his paper in this *Journal*, vol. xiii. p. 116.

maternal placenta, and which corresponded in form, size, and position to the zone on the chorion. This zone contained multitudes of short cylindriform crypts, in which the numerous short villi of the chorion were lodged. Longer and more deeply placed crypts were also present for the lodgment of the longer villi.

The non-placental area of the mucous membrane was smooth, and corresponded to the non-villous part of the chorion.

Uterine glands were seen both in the placental and non-placental areas of the mucous membrane. In the placental area they opened amidst the crypts by special orifices; in the non-placental area they opened obliquely on the smooth surface of the mucous membrane.

Owing to the shortness both of the chorionic villi and the uterine crypts and their simple form, it is believed that the placenta, when shed in normal parturition, would be generally non-deciduate, in the sense that the vascular walls of the crypts would not be shed along with the villi; it is not unlikely, as the author showed some years ago to be the case in the sheep and cow,[1] that the epithelial lining of the crypts may separate more or less, and pass off entangled between the villi; also it is possible that the longer villi might carry along with them parts of the vascular walls of their crypts.

Should the placenta be non-deciduate in the sense that the vascular part of the maternal mucous membrane is not shed, during parturition, then the placenta of the Dugong gives a new type of placenta—one which is both zonary and generally non-deciduate.

The diffused character of the placenta in the specimen described by Paul Harting was due to its comparatively early stage of development, for the villi had not as yet limited themselves in it to a definite zone.

The paper concluded by a comparison of the placentation of the Dugong with that more especially of the Cetacea, Carnivora, and Proboscidea, and by remarks on the bearings of the form and structure of the placenta on the classification of the Sirenia.

[1] *Proc. Roy. Soc. Edin.*, May 1875.

TUBERCULOSIS IN VERTEBRATES. *From the Pathological Institute of the University of Strassburg* (Prof. VON RECKLINGHAUSEN). By WALTER K. SIBLEY, M.B. Camb.[1]

1. *Tuberculosis in Snakes.*—I have been unable to find in literature any description of tuberculosis in reptiles, with which I could compare the following data; it therefore needs strong grounds to enable one to describe the interesting case in question as one of true tuberculosis.

An example of (*Tropidonotus matrix* var. *murorum*, a native of Italy) died in a zoological garden after a few months' captivity.

Externally, there were on the right side of the body three prominent tumours about the size of hazel-nuts; these being firmly attached to the ribs, one of them enclosing some seven ribs in its substance. The skin, which was adherent to the tumours, was apparently unchanged. Also numbers of other smaller subcutaneous deposits the size of peas adherent to the skin, but not visible from the exterior, were seen upon removing the cuticle. These occurred generally scattered over the whole extent of the reptile. In addition to these many small nodules were found in the body-cavity along the whole length of the animal on the sides of the vertebral column between the layers of loose fascia here present. These deposits existing in front of the vertebral column along the posterior surface of the lung, are not adherent to the walls of its sac. One at the commencement of the dilatation of the bronchus is, however, firmly adherent to it. Deposits of a similar nature occurred in the corpus adiposus about the kidneys.

There was also a complete chain of small nodules firmly attached to, and often more or less surrounding the upper part of, the aorta, extending from the junction of the two arches on the left side of the body to the lower end of the liver. Along the remainder of its course no other nodules were seen.

Upon section, all the deposits appeared to be composed of caseous material.

The *Heart* and *Lungs* presented no obvious lesion.

The *Liver* was slightly enlarged, the capsule not much thickened, and the substance of the organ studded throughout its extent with small nodules mostly the size of a pin's head; others attained the size of peas, and these appeared as caseous when cut. Many of these deposits were readily separated from the liver substance as roundish masses, often with smaller nodules attached to them, and appeared when removed from the liver tissue to be filling and lying in smooth-walled cavities. These deposits were more abundant in the dorsal than the ventral part of the organ. Sometimes two or more small ones were firmly attached to the walls of vessels; these occurred on the branches of the portal vein lying in the liver.

The *Spleen* was found profoundly changed, its tissues being hardly recognisable.

The *Pancreas*, with the naked eye, presented no obvious lesion.

The *Digestive Tract*, especially opposite the lower end of the liver, pre-

[1] This paper originally appeared in German in *Virchow's Archiv*, Bd. 116, 1889, and has now been translated with the kind permission of the Editor.

sented some nodular enlargement in its walls. Some deposit also occurred in the walls of the lower end of the stomach, with thickening of its outer coats.

The *Intestines* were found all firmly mattened together by adhesions, the blood-vessels here dilated and full of blood.

In the *Rectum* small nodules occurred in the serous coat, but not implicating the muscular.

No deposits were seen in the *Mesentery* or *Peritoneum*.

The *Kidneys* and the *Reproductive Organs* contained nodules of the same nature as those described above.

MICROSCOPICAL APPEARANCES. — The *Liver*, as above mentioned, is studded throughout with deposits, all of which, in section, appear more or less round.

The smallest deposits consist of a collection of small cells with little or no fibrous tissue around them, so that they are not distinctly marked off from the liver cells in their immediate neighbourhood. Most of them show foci of degeneration not always occurring in the centre, and sometimes multiple. The larger nodules consist usually of a small central hyaline degenerated area crowded with bacilli, and whose margins are often irregular with processes extending out into the next zone. The central region of this patch appears homogeneous. Towards the periphery, however, many small deeply staining granules are seen, and outside these a few small cells occur.

The area of degeneration, with its peripheral small-celled infiltration, passes more or less imperceptibly into an outer zone consisting of large branching cells, whose nuclei alone stain slightly; these forming a loose meshwork of clear tissue, scattered among the interstices of which are a very varying number of small cells. These large unstaining branched cells often occur between the above mentioned processes of the central degenerated tissue. In this zone of branching cells smaller foci of degeneration are frequently seen. The boundary of the nodules is formed by a ring of fibrous tissue infiltrated with small cells. Outside this the liver cells generally appear more or less normal.

In places where a large number of deposits occur without intervening liver substance, each individual nodule exhibits the same appearances as just described in the case of the solitary ones; the relative amount of degenerated tissue in the individual constituent deposits being apparently unchanged.

In all the deposits giant and epithelioid cells are conspicuous by their absence.

In all these deposits large numbers of tubercle bacilli are present. In the smallest, they occur regularly scattered throughout the whole tissue. In those which reveal foci of degeneration, the bacilli appear crowded in these spots. Although occurring sparingly elsewhere, they exist to, and sometimes penetrate, the encapsuling fibrous tissue, being occasionally present among the changed liver cells in the immediate proximity of the deposits. In the nodules in which degenerative processes are still more advanced, one finds bacilli scattered thickly in the peripheral parts of these areas, but are absent from the central or older regions of degeneration, as I have previously described to occur in Birds.[1] Occasionally there occur structures consisting of a central mass of hyaline degenerated tissue of varying consistency, arranged in concentric rings; this is immediately surrounded by a broad zone of small closely disposed well-staining epithelioid cells, the whole being quite round and encapsuled by fibrous tissue. No bacilli appear to be present either in the central or peripheral regions of these structures.

[1] Author's "Tuberculosis in Fowls," *Trans. Path. Soc. Lond.*, 1888.

The structure of the deposits in the other viscera and in the connective tissues being practically the same as the description given in the case of the liver, it is unnecessary to describe them at length.

With regard to the *Lungs*, no changes are recognised in the pulmonary tissue immediately overlying the nodules in relation to it.

The *Spleen* was full of deposits, between which but little of the intact splenic pulp remained.

In the *Pancreas* a few small deposits occur in its substance, usually in close proximity to the arterial branches.

The only well-marked deposit affecting the mucous membrane of the *Digestive Tract* appears in the lower end of the stomach, where in the substance of some of the rugæ changes of a similar nature occur, and bacilli abound here. They are also seen in some small grit-like depressions on the surface of the mucous membrane.

The small *Subcutaneous Nodules* present a central necrotic area, which is comparatively more extensive than that of the deposits in the viscera, and the small-celled infiltration around it is more abundant. The central necrosis is arranged in irregularly concentric layers, between which are roundish areas of hyaline. Scattered through this district are also clear patches of albuminous matter with small corpuscles, and occasionally blood-corpuscles and fibrine. Outside this there is considerable small-celled infiltration into the zone of clear branching cells, and here one finds hyaline patches of degeneration, and many vessels probably lymphatics containing small lymph corpuscles, and with considerable infiltration in and around their walls. Bacilli are not abundant in the layers of necrosis, but are very numerous in the roundish hyaline areas; none are seen in the clear albuminous patches occurring in the same. They are found plentifully in the hyaline foci in the external zone, being especially abundant in the tissues around the vessels.

The *Tumours* in relation to the ribs are characterised by greater vascularity, and are composed partly by large clear albuminous patches with fibrine, many small cells, and occasionally blood-corpuscles, and partly of a tissue of the same nature as described in the case of the deposits in the liver. Bacilli are again crowded in all the hyaline patches, but are absent from the albuminous ones.

Upon section through the *Aorta* and its contiguous thrombosed lymphatic, one finds considerable proliferation of the endothelium of the former along a line corresponding to the attachment of the lymphatic vessel. Bacilli abound in the muscular and serous coats of this segment of the aorta. The contents of the neighbouring vessel are of the same nature as the deposits occurring elsewhere.

From the description of this case, it is seen that we have, without a doubt, *granulomata* with central necrosis. And, moreover, in these bacilli abound which, in respect to their microscopical characters and reaction to staining reagents, would appear to be the same as those which in Man and higher animals are known as tubercle bacilli.

After this appears the diagnosis, which was given in the heading of general tuberculosis fully warranted. Whether the disease had a local origin or not, my work gives no definite information. On the other hand, so far as the seat of the tubercular deposits is concerned, there can be no doubt that those in relation to the aorta were in the lymphatic vessel; also in the viscera, they are distinctly encapsuled as if by a vessel wall; but it is noteworthy that in sections they always appear round, never oval or elongated. Again, the structure of these deposits in the viscera was the same as that of the lymphatic vessel by the aorta. So we can, on good grounds, conclude that the primary seat of the disease is found in the *lymphatic system*.

2. *Tuberculosis in Birds.*—Most of the literature on this subject deals with the disease as it occurs in the domestic fowl. The two cases I am about to describe serve to illustrate its spontaneous development in the two great classes of birds, viz., Graminivorous and Carnivorous.

The following case of a Peacock appears to be a very good example of the occurrence of tuberculosis in a graminivorous bird, being associated in this case also with bone disease, and, a point especially worthy of note, with very extensive amyloid degeneration :—

The bird was extremely emaciated, and presented several tumours of a caseous nature, often as large as walnuts, on various parts of the body. A large one was situated on the back, firmly attached to the inferior angle of the scapula. A second mass, not quite so large, was found between the planes of the muscles in this region. Another was perforating the vertical plate of the sternum towards its lower end. A mass of the same nature was seen on the inner surface of the ribs, producing their complete absorption.

The right knee-joint was beset with large masses, one the size of a walnut being attached to the anterior surface of the patella. Another, smaller, was on the inner side of the joint adherent to the capsule. In addition to these, many small nodules were found growing from the muscular tendons inserted in the neighbourhood of the joint. A nodule with a loose central mass was found situated in the popliteal space, with considerable adhesion and thickening of the surrounding tissues. Upon opening the joint, little or no fluid was present in the interior. The synovial membrane was considerably metamorphosed, in places hypertrophied and pigmented, and containing numbers of small white bodies in its substance. The cartilages were soft and gelatinous. A small sinus led from the cavity of the joint into the substance of the external condyle. Upon making a section through the shaft of the femur, it was found to be exceedingly thin, only a few long spicules stretching across its interior. A large soft mass was discovered in the substance of the external condyle, with the above-mentioned sinus connecting it with the joint.

There was no obvious lesion to be discovered in the other joints. A caseous mass was present in the right side of the neck, distinct and free from the œsophagus or the trachea. A deposit, the size of a pea, occurred on the external surface of the pericardium.

Another caseous mass was found projecting from the walls of the superior vena cava immediately above its entrance into the pericardium, and separated from the lumen of the vessel by a thin membrane. Upon opening the *Heart* considerable thickening of the mitral valve was seen.

The *Liver* was somewhat enlarged, its surface smooth, having a pale and waxy appearance upon section. Its substance was studded with yellowish-white miliary deposits.

The *Spleen* was also somewhat enlarged, and contained deposits which were larger than seen in the liver.

The *Kidneys* were pale, surface slightly irregular, and exhibiting a few small deposits in their substance.

The *Digestive Tract* was considerably affected with nodular enlargement of its walls; one occurred in the œsophagus, several in the duodenum, while isolated deposits were seen in the mesentery. The cæca, contrary to what is usually found in fowls, were free from deposit, they being abnormally full of fæces.

Microscopical Appearances.—In the *Liver*, in parts, the cells of the organ are considerably altered, their outlines being indistinct and their nuclei not visible. The whole tissue has a dull and opaque appearance, staining very imperfectly. Between the lobules are a few small cells, and

in places vessels filled with corpuscles. All the connective tissue and wall of the vessels have an opaque and homogeneous appearance.

Scattered through the tissue are some small more or less round deposits, consisting of a central giant cell surrounded by granulation tissue. Others rather larger occur, which consist of one or more central giant cells together with large cells with indistinct nuclei; these are again surrounded by cells of an epithelioid nature with their long axes usually circularly disposed, and these by a zone of small round cells. The whole granuloma is destitute of a distinct fibrous capsule.

In most of these some degenerative change is in progress in the central area, and often is clearly beginning in the giant cells, the protoplasm of many of which is undergoing hyaline degeneration, in the substance of which the numerous nuclei remain for some time distinctly visible. Larger structures occur in appearance as thrombosed vessels; these contain in the centre an irregular hyaline mass, between the peripheral processes of which are numbers of giant cells. Surrounding these is a zone of granulation tissue, the granuloma being enclosed as if by a thickened vessel wall, on the inner surface of which more giant cells are sometimes seen.

It would appear that various stages from the small deposits above-mentioned to these apparently thrombosed vessels can be traced with epithelioid and sometimes giant cells, the whole appearing to be produced from a proliferating endothelium. The endothelial lining, however, of most of the vessels, as the portal vein, hepatic artery, and bile ducts, appear more or less normal.

With the iodine solution, the connective tissue and walls of the vessels, together with many of the liver cells, give the mahogany-brown colour which deepens on the addition of sulphuric acid. With methyline violet the same regions stain red, the various deposits staining blue.

No bacilli could be found in any of the liver deposits.

The *Splenic* tissue is profoundly altered, the walls of the vessels being considerably thickened, and in some cases thrombosed. On examining more minutely one of these thrombi, one finds the original vessel-wall existing as a fibrous capsule, containing in places an artery with thickened walls in its substance. Within this is a broad zone of connective tissue with a few vessels and epithelioid cells, often in groups, and isolated giant cells, with here and there an irregular patch of hyaline degeneration. As we approach the centre, a zone of flattened epithelioid cells presents itself, within which again is a ring of giant cells, the centre of the whole being formed by a mass of degenerated tissues in which sometimes bacilli occur.

The whole of the splenic pulp and the blood-vessels give the amyloid reactions.

In the *Kidney*, the cells of the tubules appear to be normal. Many of the glomeruli have undergone change and present an opaque appearance. A few thrombosed vessels are present. With the iodine solution all the blood-vessels—both those of the glomeruli and of the tubules—give the amyloid reaction. With methyline violet it is seen that the amyloid change has affected especially the blood-vessels and the glomeruli, the connective tissues of the tubules, also, to a certain degree.

Upon section the mitral-valve of the *Heart* presents considerable myxomatous thickening of its substance. The pericardial tumour consists of a central caseous necrosis surrounded by a broad zone of tissue much infiltrated with small cells; around the circumference of the necrotic tissue are numbers of giant cells.

In the broad zone are numbers of groups or nests of epithelioid cells. Giant cells are also present, scattered irregularly about, the rest of the nodule being made up of small cells and fibrous tissue, in which hyaline globules are occasionally present. A few blood-vessels with changed walls are present in parts of the growth. Bacilli are present in parts of the

caseous centre, but do not appear to exist in the tissue outside this. The structure of the larger tumours attached to the fibrous tissues around the bones and between the muscles is formed of a tissue of the same constitution, but with several foci of caseous degeneration of various stages, each having usually several giant cells immediately surrounding it. Bacilli do not appear to be present either in the giant cells or in the epithelioid cell-nests, and only sparingly in the clearer parts of the caseous masses.

The mass in the popliteal space is formed of the same sort of tissue, but contains many more large hyaline globules, and in its centre is a mass of small cells like that of a lymphatic tissue. No bacilli are found in this nodule.

The soft mass in the substance of the external condyle consists of a collection of granulation tissue, which in places has undergone caseous and hyaline degeneration. A few epithelioid cells are present, also a few giant cells scattered about, together with many albuminous and fatty globules. Blood-vessels filled with corpuscles are also numerous.

Sections through the synovial membrane of the diseased knee-joint show the serous membrane to be much metamorphosed. The endothelial cells appear to be replaced by a granulation tissue, the cells of which are much swollen, forming globules which give the amyloid reactions. On the surface occur many granulomata, some of which are undergoing central degeneration. These are the small white bodies which were noticed in the description of the macroscopic appearances.

From the class of carnivorous birds I have taken a case occurring in a *Barn Owl*, originally from Africa, which died after a few months' captivity.

In this case, as in the former, the bird was extremely emaciated. Upon opening the abdominal cavity the surface of the viscera was seen to be studded with small white bead-like bodies, the size of large pins' heads. These were especially abundant in the neighbourhood of the stomach.

The *Liver* was not much enlarged, its surface smooth, and upon section no obvious deposits were to be seen in its substance.

The *Spleen* was enlarged, surface irregular, and its substance appeared to be full of minute yellowish-white granular deposits.

In the *Pancreas* some opaque spots were seen, especially in the central regions of the organ.

The *Heart*, *Lungs*, and *Kidneys*, presented no naked eye lesions.

The mucous membrane of the *Stomach* appeared normal, but in the commencement of the duodenum a deep somewhat circular ulcer the size of 6 mm. presented itself. The edges were considerably raised and jagged, the surrounding tissues being infiltrated and thickened. Its floor showed small irregular masses of necrotic tissue, while the peritoneum over it was thickened and opaque. Lower down the intestines some small irregular patches occurred with thickened mucous membrane, but without apparent ulceration of its surface.

Microscopical Appearances.—The *Liver* vessels are numerous and filled with blood, and the whole section appears densely studded with small areas, the majority of which appear round in section; occasionally they are seen oval or elongated. Each area is composed of a group or nest of nucleated and very granular cells of an epithelioid nature, the whole being distinctly encapsuled by bands of fibrous tissue. In some parts of the organ the deposits are so densely packed as to exhibit little or no intervening liver substance, but in no case do the individual deposits appear to fuse together, and no caseous substance is to be seen. When subjected to the methods for demonstrating the presence of tubercle bacilli, all these areas are found to be crowded, and the bacilli appear to abound in the epithelioid cells them-

selves. The walls of the liver vessels, viz., portal vein, hepatic artery, and bile ducts, appear normal.

The whole substance of the *Spleen* is likewise densely studded with areas of the same nature as those found in the liver. All these are again crowded with bacilli, and bacilli also occur isolated and in groups, apparently in the splenic tissues outside these areas.

In the *Pancreas*, the mass of secreting tissue of which appears normal, areas occur which are sometimes small and round, at other times large, but with regular outlines. These consist of a degenerated unstaining tissue containing several staining granules, and is arranged in lobuli as the secreting tissues of the organ, and in places it would appear to partly consist of changed pancreatic cells. In these areas the outlines of the original alveolæ is lost, the whole appearing much degenerated. No bacilli are present in any of these areas.

Sections through the walls of the *Stomach* reveal nothing abnormal. A section through one of the thickened patches in the small intestine exhibits a very considerable infiltration of the mucous membrane and new tissue formation. The formation consists almost entirely of groups of epithelioid cells, often round, but here frequently extending in columns between the tissues of the mucous membrane, and more or less vertical to the walls of the gut. The muscular and serous coats are thickened and much changed in the region of the growth, and occasionally groups of epithelioid cells are seen scattered through the substance of the muscular and serous coats, appearing as if they found their seat in vessels. All these epithelioid cells which form the mass of the mucous membrane tumour, and exist in the muscularis and the serosa neighbouring there, also likewise contain large numbers of tubercle bacilli as those cells of the splenic deposits.

A vertical section through the duodenal ulcer shows the base to be formed by the muscular coat, which is infiltrated with small cells and granular epithelioid cells in groups. Irregular caseous masses are seen scattered through its substance, and also some occur on the surface of the ulcer. The edges of the ulcer are seen to consist of the mucous membrane much altered by infiltration of epithelioid cells. Here again bacilli abound in all the epithelioid cells, being especially numerous in the periphery of the caseous nodules, none occurring in the centres of the same. For demonstrating the presence of bacilli, I used the following methods :—

1. The sections were placed for two hours in Ziehl's solution of fuchsine and carbolic acid, and then washed with 5 per cent. sulphuric acid till all the colouring matter disappeared from the tissues, then washed in water, afterwards still further decolorised in alcohol, then through cedar oil and mounted in balsam. Instead of sulphuric acid sometimes 30 per cent. nitric acid was used.

By these means I succeeded in completely decolorising the tissues, but the bacilli, even after long treatment with acid, always retained the colour.

2. *Weigert's Method.*—The sections were placed for twelve hours in a solution prepared by shaking aniline oil up in distilled water and filtering, to which a few drops of methyline violet are added. From this solution the sections are removed into salt solution, and then two to three minutes in iodine solution, and then dried. After this they were completely discolorised with aniline oil, and then through xylol, and mounted in balsam. Sometimes the sections were previously stained with alum carmine.

Since the bacilli which have been stained by these methods exactly resemble in form and colour those which in man and higher animals are recognised as tubercle bacilli, one has good grounds for asserting that they are identical with the latter. Accordingly, one must consider the same as tubercle bacilli, and the case as one of tuberculosis. Although I found no caseous degeneration in the deposits, even in the

epithelioid cells, the nuclei and the cell boundary were well preserved, and only in the case of the duodenum did degenerative processes occur, and here an ulcer was found. Apart from the presence of genuine bacilli, I found, even in the connective tissues between the deposits of epithelioid cells, a large number of round cells, so that one must reckon the whole process as lymphomatous or granulomatous tissue formation. In all cases the bacilli found in the distinctly preserved epithelioid cells, which in many respects so closely resemble the *leprous bodies*, are of great interest for the whole theory of the diseases produced by bacteria.

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NOTES OF A CASE OF PERSISTENT LEFT SUPERIOR VENA CAVA, THE RIGHT SUPERIOR VENA CAVA BEING IN GREAT PART A FIBROUS CORD. By J. J. CHARLES, M.D., *Professor of Anatomy and Physiology, Queen's College, Cork.*

IN a middle-aged and fairly nourished subject, dissected in the Cork College last winter, the following rare abnormalities of the veins of the thorax were observed by me:—

The Innominate Veins were of the usual size, but transposed. The *right* vein was long, and took an oblique direction over the roots of the arteries arising from the arch of the aorta, whilst the *left* vein, which was short, lay nearly parallel to the left subclavian artery, and joined the *right* vein to form the *left superior vena cava.*

The Left Superior Vena Cava crossed the arch of the aorta by the side of the inferior laryngeal nerve, then over the root of the left lung to the groove between the left auricle and ventricle, and terminated in the right auricle by a large oval aperture.

The Right Superior Vena Cava lay above by the side of the aorta, and then crossed the front of the root of the right lung, where it was merely a fibrous cord, with an imperfect or incomplete vestigial fold around it; and at its lower end it was connected with the right auricle, where it was patent for a short distance. In the middle of its course it could not be properly dissected out on account of its firm adhesion to some calcified lymphatic glands.

The Vena Azygos Major received nearly all the intercostal veins of the left side, and then passing over the upper part of the descend-

ing aorta, terminated in the *left superior vena cava* below the level of the transverse portion of the arch.

The Azygos Veins of the Right Side—upper and lower—ended in the large azygos vein on the left side; the *lower* one, which, as usual, was the larger, received the intercostal veins of the right side as high as the ninth space; and the *upper* one, those on the same side, from there up to the third space.

The Superior Intercostal Veins were transposed at their terminations.

The Inferior Vena Cava was normal; so also were the *Aorta* and its *branches*.

The *Heart* itself was firm and well developed, but the *left ventricle* seemed to occupy more of the anterior surface than usual.

The *Viscera* were not transposed.

There are only a very few cases similar to the above on record.

ABNORMAL DEVELOPMENT OF GENITO-URINARY SYSTEM OF *LEPUS CUNICULUS*. By Oswald H. Latter, *Assistant to the Deputy Linacre Professor of Human and Comparative Anatomy, The Museum, Oxford.*

A somewhat remarkable abnormality was noticed a short time since in a Rabbit which was being dissected by one of the students in this department. This abnormality consists in the entire absence of generative organs from the right and of excretory organs from the left side of the body. The right kidney is rather unusually large, its length being 1½ inch and its greatest breadth 1⅛ inch, and its breadth at the hilus ⅞ inch. But there were among the other rabbits dissected several which possessed both kidneys nearly as strongly developed as the single one in question. There is no sign whatever either of kidney or ureter on the left side. Similarly, the ovary on the left side is well developed, but not unusually large. The Fallopian tube is normal, and the uterus of the left side alone is present. There is no trace at all of the right uterus. The suprarenal bodies are, however, present on both sides of the body. The left suprarenal is closely attached to the dorsal aorta by a stout and very short artery, which is not usually present. The blood vascular supply is modified in a way corresponding to the above abnormalities. The renal artery and renal vein are present on the right side of the body only, but I am inclined to regard the stout suprarenal artery to the left suprarenal body as the possible remnant of the left renal artery. I was unable to ascertain the exact arrangement of the ovarian vessels, and have accordingly omitted them from my drawing. I may add that the Rabbit was full grown, and to all appearance in sound health, nor in any way inconvenienced by the loss of normal bilateral symmetry.

In my drawing I have represented the bladder pulled over somewhat to the right side, so as to show the ureter entering as nearly as possible in the mid-dorsal line.

INDEX.

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PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

JUNE 1888.

THE Summer Meeting of this Society was held at Cambridge, on Saturday, June 23, in the Anatomical Museum of the University.—Present, thirty-eight members and visitors. Professor HUMPHRY in the chair.

Professor MACALISTER showed a series of specimens which had been obtained from the Cambridge dissecting-room. They included *Abnormalities* of the skeleton, muscles, arteries, veins, and digestive tract.

Professor CURNOW showed an *Asymmetrical Skull* which presented the following abnormal features:—

The right half is obviously larger than the left half, there being a difference of nearly 2 inches in the measurement between the tips of the mastoid process and the interparietal suture on the two sides, the left measuring 16 inches and the right 18. The frontal suture is to the right of the junction of the interparietal sutures. The left half of the bony palate is larger than the right, the pre-maxillary suture distinct, and the basi-occipital has not yet joined the basi-sphenoid. On the left side there is nothing special to remark; on the right side there is a distinct supra-orbital canal, running obliquely through the bone from without inwards for half an inch. Three large Wormian bones occupy the position of the ali-sphenoid and squamous parts of the temporal. The zygomatic process of the temporal bone is absent, the articulation of the jaw taking place with the most anterior of the three Wormian bones above-mentioned. The tympanic bone and the petrous portion of the temporal bone are incompletely developed, so that the auditory meatus is not separated by any bony partition from the carotid canal. In the occipital region a suture can be seen, probably marking off the limits between the membranous and the cartilaginous cranium. I exhibit this skull to show remarkable developmental anomalies of one side only.

The PRESIDENT was inclined to doubt whether the skull was hydrocephalic, and Mr WALTER PYE wished to know if the asymmetry was unusual.

Bulbo-cavernosi Muscles in Women.

Dr Symington exhibited some coronal sections through the anterior part of the pelvis of a female, about 50 years of age, to illustrate the position and relations of the bulbo-cavernosi, or so-called sphincter muscles of the vagina. Each muscle was about 1·5 mm. in thickness, and was placed external to the vestibular bulb. It was obvious, from their position and size, that they could have no appreciable effect in closing the vaginal orifice.

These sections also showed the relations between the pudendal and vaginal slits. The former is essentially a vertical mesial slit, while the latter is a transverse one. One of the sections passed through the bladder, the urethra just behind its external meatus, the vestibular bulbs, and the labia majora and minora. This section was rather more than $\frac{1}{2}$ an inch in front of the perineal body. Another section was made $\frac{1}{8}$ of an inch behind the preceding one. It divided the bladder, vagina, and perineal body.

In the more anterior of the two sections the pudendal cleft appeared in the form of a mesial slit about 1 inch in length, but above this it divided into two limbs, each limb being $\frac{3}{8}$ of an inch long. The whole space was thus Y-shaped. In the posterior section the vaginal cavity appeared as a transverse slit $1\frac{3}{8}$ of an inch in length.

These two sections were made upon the frozen cadaver, but the mass of tissue between them was hardened in spirit, embedded in celloidin, and cut with a large microtome into a series of moderately thin sections. An examination of this series showed that the two limbs into which the pudendal cleft divided gradually increased in length, and became more horizontal as they approached the vaginal orifice.

Demonstration of Auditory Air-Passages.

Dr Symington also showed a frozen section of the head, which he had found useful in demonstrating the air-passages connected with the ear. In preparing the specimen, the head was divided horizontally at the level of the external auditory meatuses. In front of these a cut was made downwards and forwards, so as to open the Eustachian tubes in their whole length. This oblique incision was joined at the naso-pharynx by a horizontal section made from before backwards a little above the floor of the nose. The specimen afforded a connected view of the external auditory meatus, tympanic cavity, Eustachian tube, naso-pharynx, nasal cavity, and nostril.

It was explained that sections of this kind were prepared more easily in children, in consequence of the more horizontal direction of the Eustachian tubes in early life.

Two Adult Temporal Bones, with Non-union of the Squamous and Petro-mastoid Portions.

Dr Symington met with these specimens in a disarticulated skull purchased from a dealer. The bones were evidently those of an adult,

as all the teeth were erupted, and the basi-occipital and basi-sphenoid had been separated by a saw.

None of the bones of the skull presented any peculiarity except the two temporals, and the condition of these was practically identical.

Each temporal bone consisted of two parts, one formed by the united petro-mastoid, tympanic, and styloid elements, the other by the squamosa. Although these two parts were movable one upon the other, they could not be completely disarticulated owing to some interlocking of the tegmen tympani with the squamosa.

In each specimen the line of union between the squamosa and the other parts of the temporal could be traced on the surface of the bone as follows:—From the incisura parietalis (or notch between the upper convex border of the squamosa and the upper edge of the mastoid) it passed downwards and forwards to the anterior part of the mastoid process, then turned upwards in the posterior wall of the external auditory meatus immediately behind the tympanic bone, and went over the inner extremity of the roof of the meatus to the Glaserian fissure. At the outer part of this fissure it lay between the tympanic plate and the post-glenoid process, but more internally it was separated from the tympanic plate by a process of the pars petrosa. From the inner end of the Glaserian fissure the suture could be traced backwards, on the inner surface, to the incisura parietalis.

Fig. 1 shows the line of union on the outer and under aspect of the bone.

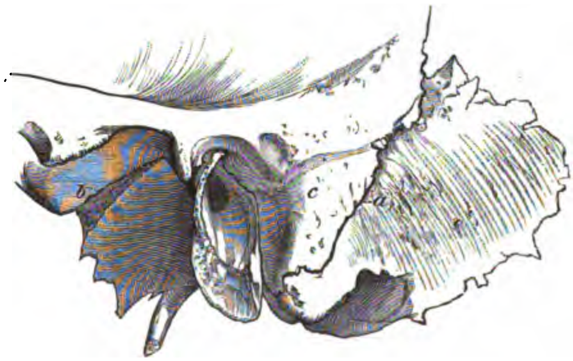

FIG. 1.—*a*, squamoso-mastoid or external petro-squamous suture; *b*, above inner extremity of Glaserian fissure; *c*, post-auditory process of the squamous portion of the temporal.

The suture extending downwards and forwards on the outer surface of the bone from the incisura parietalis to the anterior border of the mastoid process (see *a*, fig. 1) is usually called the squamoso-mastoid suture. This name, however, is rather a misleading one, for the suture goes across the mastoid, and divides it into two portions. Since the mastoid part of the temporal bone is formed from the post-auditory process of the squamosa and the outer part of the pars

petrosa, it is more correct to call the suture between them the external petro-squamous. The line of union between the squamous and petrous portions, which is seen on the inner or cranial aspect of the temporal bone, may be termed the internal petro-squamous suture. In 1867, J. Gruber[1] of Vienna directed special attention to the dual origin of the mastoid and the practical importance of its outer aspect in connection with inflammatory conditions of the middle ear. The persistence to a greater or less extent of this suture in the adult is by no means uncommon.

Cloquet,[2] Aeby,[3] Leidy,[4] and others, give drawings showing its presence in the adult. Kirchner[5] examined 300 adult skulls in order to ascertain the frequency of its occurrence. He found it well marked on both sides in 5 per cent. of the cases. The suture is very distinct at birth, but generally becomes obliterated before the end of the second year.

On the left side the squamosa was disarticulated from the remainder of the temporal bone. In order to effect this, it was necessary to break a few small processes of the tegmen tympani. Fig. 2 shows an

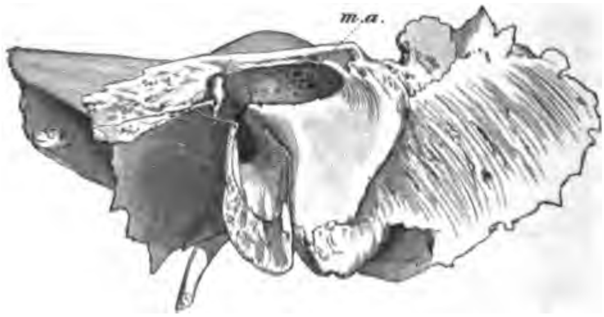

FIG. 2.—*m.a.*, mastoid antrum.

external view of the temporal bone after the removal of its squamous portion. The attic or upper chamber of the tympanic cavity and the mastoid antrum are exposed, as the squamous portion forms the outer wall of these spaces. The openings of the mastoid air-cells into the antrum are numerous but small, none of them being more than two or three millimetres in diameter. Below and behind the antrum is seen a smooth triangular surface, which articulated with a corresponding smooth surface on the inner aspect of the post-auditory process of the squamosa. A comparison of figs. 1 and 2 will serve to show the relation between the mastoid antrum and the outer surface of the temporal bone.

The Eustachian tube is generally described as being situated in

[1] *Wiener med. Wochenschrift*, 1867, s. 851.
[2] *Anatomie de l'homme*, 1821, tab. xiv. and xxvi.
[3] *Der Bau des menschlichen Körpers*, Leipzig, 1871, fig. 86.
[4] *Science*, vol. i. p. 507.
[5] *Arch. f. Ohrenheilkunde*, 14 Bd., 1879.

the receding angle between the petrous and squamous portions of the temporal. The tube, however, lies a little internal to that point, and has its walls formed entirely by the petrous and tympanic parts of the temporal.

The malleus remained in position after the left temporal had been disarticulated. Its processus gracilis was well developed.

Complete absence of osseous union between the squamous and the other parts of the temporal bone, although of normal occurrence in many mammals, would appear to be extremely rare in the adult human subject. Numerous cases have been described of partial persistence of the sutures between the different elements of the temporal bone, but I have failed to find any record of complete non-union, such as exists in these specimens. In the human subject the annulus tympanicus unites with the squamous sooner than with the petrous portion of the temporal, but in my specimens the tympanic bone, although separable from the squamosa, is firmly ossified to the pars petrosa.

Professor THANE considered that in this case the squamo-temporal was quite absent and replaced by Wormian bones.

Spinal and Cranial Nerves.

Dr GASKELL gave a short sketch of the results of his recent observations on the structure of the spinal and cranial nerves, and pointed out that the cranial nerves, with the exception of the nerves of special sense, were built up on the same plan as the spinal nerves, and arose from similar groups of nerve cells in the central nervous system. The cranial nerves differed, however, from the spinal in that they were divisible into two great groups, viz.,

Group I. Composed of the oculomotor, trochlearis, abducens, motor part of the trigeminal, and facial nerves,—a group composed of at least four complete segmented nerves, each of which had lost their posterior root and root ganglion, but retained to a greater or less extent the rest of the components of a special nerve.

Group II. Composed of the sensory part of the trigeminal, glosso-pharyngeal, vagus, spinal accessory, and hypoglossal nerves—nerves which make up a large group of at least five complete segmental nerves, which are in origin partly cranial and partly spinal, which are extensive in their distribution, which have lost none of their components, but the different components have largely become separated to four separate nerve roots.

The author then proceeded to point out that an explanation must be found in the past history of the vertebrata for the two great and most striking peculiarities of these two groups of cranial nerves, and he ventured to put forward a theory to account for the degeneration observed in Group I., leaving for a future occasion the consideration of the peculiarities of Group II.

Taking first into consideration the structure and development of the spinal cord, he suggested that the segmental arrangement of the nerves was bound up with a segmental arrangement of the groups

of ganglion cells which gave origin to those nerves; so that, as far as the nervous part of the spinal cord was concerned, it might be looked upon as a bilateral chain of ganglia, which were connected with each other by nerve fibres, and gave origin to a series of segmental nerves. In addition to this bilateral chain of ganglia, there is found in the spinal cord a meshwork of supporting tissue, which forms a tube in the meshes of which the nervous elements are inserted. He ventured to suggest that this tube of supporting tissue was formed by the folding over of the medullary plate to form the neural canal, and he pointed out how the non-nervous character of this tube is exemplified in the roof of the 4th ventricle, in the roof of the sinus rhomboidalis of birds, and in the neurenteric canal, by means of which the neural canal is continuous with the alimentary canal.

Further, he gave reasons to show that this neural canal had originally an anterior opening, which was at the extremity of a small tube leading into the cavity of the infundibulum, the walls of which, by being pressed down on to the tuber cinereum, had come together, and so occluded the opening of the tube.

He pointed out how the arrangement of the nervous tissue of the brain and spinal cord around this tube of supporting tissue corresponded to the arrangement of the invertebrate nervous system, in which the cerebrum, cerebellum, and those parts of the brain which are dorsal to this tube represent the supra-œsophageal ganglia and give origin to the nerves of special sense; the crura cerebri and the peduncles of the cerebellum represent the œsophageal commissures; the origins of Group I. of the cranial nerves, the infra-œsophageal ganglia; the medulla oblongata and spinal cord, the ventral chain of ganglia; while the tube itself represented the alimentary canal of the invertebrate.

Finally, he suggested the degeneration observed in Group I. of the cranial nerves was associated with the loss of the original alimentary canal and mouth parts, while the peculiarities of distribution and origin of Group II. were associated with the formation of the new alimentary canal.

The author stated that the full paper will appear shortly in the *Journal of Physiology*.

Professor HOWES could not accept Dr Gaskell's conclusions. He thought the arthropods were not the vertebrate ancestors, but that worms were in the direct line.

Dr ALEXANDER HILL wished to know whether Dr Gaskell considered the neuroglia to have been derived from mesoblast, and the nerve substance from epiblast.

Mr SUTTON could not account for Auerbach's and Meissner's plexuses, and thought them difficulties in the path of those who assumed that all nerve substances sprang from epiblast.

Dr GASKELL, in replying to the various questions, wished to point out that it was possible to look upon the spinal cord as not necessarily a nervous tube.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

NOVEMBER 1888.

THE First Annual Meeting of this Society was held on Wednesday, November 7, 1888, in the Library of St Thomas's Hospital. The President, Professor HUMPHRY, F.R.S., in the chair. The following gentlemen were elected officers for the ensuing year:—*President*—George Murray Humphry, F.R.S. *Vice-Presidents*—Sir William Turner, F.R.S.; Daniel John Cunningham, M.D.; J. D. Thane. *Treasurer*—Charles Stewart. *Secretaries*—C. B. Lockwood (England); David Hepburn, M.D. (Scotland); H. St John Brooks, M.D. (Ireland). *Council*—William Mitchell Banks, M.D.; John Curnow, M.D.; J. N. C. Davies-Colley; John Struthers, M.D.; Frank Beddard; John Cleland, M.D., F.R.S.; G. B. Howes; John Langton; John Wood, F.R.S.; A. M. Paterson, M.D.; Thomas Pickering Pick; Johnson Symington, M.D.; R. W. Reid; Rickman J. Godlee; Peter Redfern, M.D.; Frederick Treves; Alexander Macalister, F.R.S.; Bertram Windle; Alfred H. Young; Arthur Thomson.

The auditor's report had not been completed, but the Secretary was able to announce that, after all expenses had been paid, there was still a balance in hand. It was also announced that there were 125 members upon the books of the Society.

Mr GORDON BRODIE showed a specimen of an *Abnormality of the Aortic Arch*, from a dissecting-room subject. Although the varieties which it shows have all been described before, no case is on record which is precisely similar in the way in which the branches are combined, and the variations are not limited to the main trunk.

The first noticeable point is the absence of the innominate artery, and in its place a short thick trunk, which gives off two branches, ascending on either side of the trachea to take the place of the common carotids; on tracing up that on the right side, an artery is noticed given off which runs up and enters the foramen in the transverse process of the cervical vertebra (4th), in fact, the vertebral.

Next in order coming off from the arch is the vertebral of the left side, which enters the foramen in the transverse process of the 5th cervical as it courses up, and in the root of the neck a branch is given off which, passing inwards and upwards beneath the common carotid, enters the thyroid gland.

Another branch given off from the left subclavian in its first part was traced upwards to end in the tissue between the transverse processes, and was at first thought to be a second root to the vertebral; but dissection proved the fallacy. Lastly, the right subclavian was

arising from the arch as a fourth branch, and passed behind œsophagus and trachea. The right inferior thyroid came off normally.

Professor HUMPHRY read a paper on the *Angle of the Neck of the Thigh-Bone with the Shaft at various Ages and under various Circumstances*, which is printed *in extenso* on p. 273 of the *Journal of Anatomy and Physiology*. He gave numerous measurements, from which he deduced the following conclusions:—

1. That the angle formed by the neck of the thigh-bone with the shaft varies considerably in different persons at the same age.
2. That it is smaller in short bones than in long bones, and that it is usually small when the pelvis is wide, the combination of these two conditions rendering it usually smaller in men than women.
3. That the angle decreases during the period of growth, before and after birth; but that after growth has been completed it does not usually undergo any change, even if life be prolonged to extreme old age, the commonly received opinion on this point being erroneous. Some change may take place in exceptional rare cases; but, as a rule, the angle remains the same from the adult period till death, at whatever age that event may occur.
4. That if, during growth, the limb be relieved of the weight of the body, as in the bed-ridden state, in paralysis, or after amputation in the thigh, the angle of the neck with the shaft usually retains the open form of early life, or may, and frequently does, become wider.

Professor G. B. HOWES then read a paper on *The Intra-narial Epiglottis*, which is printed *in extenso* in the *Journal of Anatomy and Physiology*, p. 263.

The author records the presence of an intra-narial larynx in the common Rabbit, the conditions being similar to those previously described by him in the Hedgehog. He gives a *résumé* of all that is known upon the subject, and shows that the condition in question has been observed in eight of the twelve leading orders of living mammals. He deduces the belief that the epiglottis was primarily intra-narial, and that the velum palati was originally developed for purposes of completely shutting off the respiratory passages—the condition predominant among mammals having been due to secondary adaptation, more especially of the epiglottis, in phonation. He records the presence, in the Rabbit, of a small hyo-epiglottidean muscle which was paired as in some cetaceans (*Balænoptera*, *Globiocephalus*), and discusses its functional significance.

Professor THANE said that the arrangement described by Mr Howes was normal in man, in whom, during nasal breathing, the laryngeal orifices and epiglottis were brought up into the naso-pharynx. He argued that the epiglottis was mainly used in phonation. He could not agree that the condition described was the primitive condition.

Mr J. BLAND SUTTON referred to Dr Champney's paper on "Respiration in New-Born Children." He had found the epiglottis lying behind the palate in five fœtuses.

Mr HILL thought that food passed by the side of the epiglottis.

Mr A. THOMSON could confirm Mr Howe's observation as regards sheep, and to a lesser extent as regards man.

Professor MACALISTER also confirmed as regards man. He thought the lid cover idea of the function of the epiglottis was exploded.

A paper was read by Mr BLAND SUTTON on the *Nature of the Vocal Cords and the Hyo-Epiglottic Muscle*, in which facts were adduced in support of the contention (1) that the true vocal cords are the result of the tendinous metamorphosis of a portion of the thyro-arytenoideus muscle; (2) the false vocal cords with the cuneiform cartilages of Wrisberg are the degenerate representatives of a piece of cartilage which originally connected the epiglottis with the cornicula laryngis (Santorini's cartilage); (3) that the hyo-epiglottic ligament is the degenerate representative of the hyo-epiglottic muscle so largely developed in whales, horses, ant-eaters, many monkeys, and other mammals, sometimes even re-appearing in man. The demonstration was aided by actual dissections prepared by Mr William Pearson for preservation in the museum, at the suggestion of Professor Stewart. The paper concerned itself with actual questions of facts, and speculation was studiously avoided. (*In extenso*, p. 256 of *Journal*.)

Mr A. THOMSON said cartilages of Santorini were very large and constant in the negro.

Professor ALEX. MACALISTER could not confirm this observation.

Professor CHARLES STEWART doubted that yellow tissues could replace a muscle, as Mr Sutton argues for the vocal cord.

Mr HOWES agreed with Mr Sutton, and pointed out references which had been overlooked.

Mr J. BLAND SUTTON, in reply, mentioned muscles in which there was elastic tissue.

Mr R. W. REID read a paper on the *Relations between the Superficial Origins of the Spinal Nerves from the Spinal Cord and the Spinous Processes of the Vertebræ.* Owing to the present somewhat insufficient data afforded concerning the exact position in the adult of the superficial origin of the spinal nerves from the cord in relation to the surface of the body, he made a series of six dissections to try to localise their position more positively. He said that although the length and obliquity of the spinous processes varied a good deal, yet their posterior ends might fairly be made use of for the purpose. From examination of a number of cords, he found that for all practical purposes the posterior roots and the anterior roots of nerves belonging to the same segment left the cord at the same level. He then described the method in which the investigations were conducted —firstly, when the body was placed in the horizontal; and secondly, in the upright position. These investigations were conducted with mathematical accuracy, and the result arrived at was that the superficial origin of any individual spinal nerve had no fixed and definite relation to the apex of one, or to the apices of two of the spinous processes, or the space intervening between two, as might be supposed from the tables of Nuhn and Jadelot, but that its position varied considerably. The following was a summary of the limits within which he found

that the posterior and anterior nerve roots took their superficial origins from the cord in relation to the posterior ends of the spinous processes. (*a* signifies the highest point of origin; *b* the lowest point of origin.) Second cervical: (*a*) a little above the posterior arch of atlas; (*b*) midway between the posterior arch of atlas and the spine of axis. Third cervical: (*a*) a little below posterior arch of atlas; (*b*) junction of upper two-thirds with lower third of spine of axis. Fourth cervical: (*a*) just below upper border of spine of axis; (*b*) middle of spine of third cervical. Fifth cervical: (*a*) just below lower border of spine of axis; (*b*) just below lower border of spine of fourth cervical. Sixth cervical: (*a*) lower border of spine of third cervical; (*b*) lower border of spine of fifth cervical. Seventh cervical: (*a*) just below upper border of spine of fourth cervical; (*b*) just above lower border of spine of sixth cervical. Eighth cervical: (*a*) upper border of spine of fifth cervical; (*b*) upper border of spine of seventh cervical. First dorsal: (*a*) middle of interval between spines of fifth and sixth cervical; (*b*) just above spine of first dorsal. Second dorsal: (*a*) lower border of sixth cervical; (*b*) just above lower border of spine of first dorsal. Third dorsal: (*a*) middle of spine of seventh cervical; (*b*) lower border of spine of second dorsal. Fourth dorsal: (*a*) just below upper border of spine of first dorsal; (*b*) junction of upper third and lower two-thirds of spine of third dorsal. Fifth dorsal: (*a*) upper border of spine of second dorsal; (*b*) junction of upper fourth and lower three-fourths of spine of fourth dorsal. Sixth dorsal: (*a*) lower border of spine of second dorsal; (*b*) just below upper border of spine of fifth dorsal. Seventh dorsal: (*a*) junction of upper third and lower two-thirds of spine of fourth dorsal; (*b*) just above lower border of spine of fifth doral. Eighth dorsal: (*a*) junction of upper two-thirds and lower third of interval between spines of fourth and fifth dorsal; (*b*) junction of upper fourth and lower three-fourths of spine of sixth dorsal. Ninth dorsal: (*a*) middle of interval between spines of fifth and sixth dorsal; (*b*) upper border of spine of seventh dorsal. Tenth dorsal: (*a*) middle of interval between spines of sixth and seventh dorsal; (*b*) middle of spine of eighth dorsal. Eleventh dorsal: (*a*) junction of upper three-fourths and lower fourth of spine of seventh dorsal; (*b*) just above spine of ninth dorsal. Twelfth dorsal: (*a*) junction of upper fourth and lower three-fourths of spine of eighth dorsal; (*b*) just below spine of ninth dorsal. First lumbar: (*a*) middle of interval between spines of eighth and ninth dorsal; (*b*) lower border of spine of tenth dorsal. Second lumbar: (*a*) middle of spine of ninth dorsal; (*b*) junction of upper third and lower two-thirds of spine of eleventh dorsal. Third lumbar: (*a*) middle of spine of tenth dorsal; (*b*) just below spine of eleventh dorsal. Fourth lumbar: (*a*) just below spine of tenth dorsal; (*b*) junction of upper third and lower two-thirds of spine of twelfth dorsal. Fifth lumbar: (*a*) junction of upper third and lower two-thirds of spine of eleventh dorsal; (*b*) opposite middle of spine of twelfth dorsal. Sacral nerves—First sacral: (*a*) lower border of spine of eleventh dorsal; (*b*) lowest point of origin of fifth sacral, the lower border of spine of first lumbar.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

FEBRUARY 1889.

An Ordinary Meeting of the Society was held on Wednesday, February 6, at 5 P.M., at the Middlesex Hospital. The President, Professor Humphry, in the chair. Present, upwards of forty members and visitors. The minutes of the previous meeting were read and confirmed. Robert Bowles, M.D., &c., was announced to have been elected a member of the Society.

Mr Arthur Hensman showed a specimen to prove that the *Dorsal Artery of the Foot* crossed over the middle cuneiform bone, and not as is usually described in the text-books.

Dr St John Brooks showed for Professor Cunningham a further series of models to illustrate the *Topography of the Skull*, and read the following note by Professor Cunningham:—

Exhibition of Models.

1. Last winter Professor Cunningham exhibited to the Society a number of models, illustrative of cranio-cerebral topography.
2. These comprised the heads of two adults and several children.
3. He explained that he aimed at preparing a complete set, which would illustrate the changes which take place in the relations between cranial bones and cerebral convolutions during the growth of both.
4. At that time the series was far from complete, but now only four models are required to finish the set, viz., 2, 3, 7, 9.
5. In all he has prepared 19 human and 4 apes.
6. Up to present has failed to model the fœtal brain below the sixth month, and has had to content himself with accurate drawings of all heads younger than this. One of these, from the head of a fourth month fœtus, he begs leave to submit to the Society.
7. The difficulties connected with the safe transit of these models has prevented Dr Cunningham sending more than four models. He

has selected, however, those which he considers to be the most interesting and characteristic, viz.:—

Head of child, 6 months old.
" " new born, by breach presentation.
" fœtus, 6 months.
" ape, *Macacus rhesus.*

8. The methods adopted in preparing smaller ape brains are somewhat different from those previously detailed. Very little difficulty is experienced in hardening them without shrinkage, and nothing in these cases but spirit of different strength is employed.

A New Method of Mounting the Spine. By Prof. D. J. Cunningham.

When we attempt to articulate the separate and macerated bones of the spine so as to reproduce faithfully the natural curvature, we encounter almost insuperable difficulties. We have no means of accurately judging, in the absence of the intervertebral discs, the exact positions which the different vertebræ should take in relation to each other.

Some may consider that this is a matter of no great importance, seeing that during life there is no condition of the spinal form which may be considered absolutely characteristic. "There is not a gesture, not a change of attitude, which is not accompanied by some alteration in the curvature of the vertebral column. Our very respiratory movements, gentle and unconsciously performed as they are, meet with a response in alterations of curvature; and in the dead, when the spine is removed from the influence of the muscles—those contracting guy-ropes which help to keep it erect—when removed also from the influence of gravity, the changes which it undergoes must be very considerable."[1]

The various schematic representations which have been given, with the view of representing the typical spinal form in the living, are all more or less fanciful. That most in favour is the Horner-Meyer schema, which represents the spine in the stiff military position. This undoubtedly is a forced condition of the spine, and largely due to muscular contraction. As Krause remarks, it is only suitable for a woman well advanced in pregnancy.

The method which I have employed in articulating the spine aims at reproducing the curvature of the vertebral column as it exists in the dead. In my *Cunningham Memoir*, published by the Royal Irish Academy, I have shown that the spine may be removed from the body, and suffer no material change in its curvature, so long as the ligaments and muscles which surround it are preserved intact. This, then, is the first step in the process. The next consists in freezing the specimen, and dividing it with a saw in the mesial plane. When this is done, and while the parts are all immovably fixed in their true relative positions, an accurate tracing is taken of the cut surface. The spine is then macerated, and when the bones are clean

[1] *Cunningham Memoirs*, No. 2, by D. J. Cunningham.

a copy of the original tracing is spread out upon a board of suitable shape and size, and fixed with drawing-pins. The vertebræ are mounted on the surface of the tracing—each in its own appropriate place—and fixed to the board by two slender nails driven through each bone.

Merkel has endeavoured to reconstruct the lumbar column upon paper. He obtains an outline of the profile view of each vertebra which, from the accurate means which he adopts, may be regarded as being geometrically correct. The outlines of the vertebræ are then put in position. He assumes, in doing this, that in the attitude of anatomical rest the central points of the opposing surfaces of the articular processes must coincide with each other. Having secured the accurate coincidence of these points, he shifts the bodies of the vertebræ until they fall into a uniform curve. Upon his own showing, however, he is only able in this way to fix the position of three of the lumbar vertebræ. The first and fifth members of the group he places somewhat arbitrarily. In the case of the first lumbar vertebra, he seeks help from the Horner-Meyer schema; whilst he gives position to the fifth lumbar vertebra more or less by the eye.

Merkel claims for his highly ingenious method that it enables us to appreciate the relation which the several parts of a vertebra bear individually to the curve, and so it does. I think I may claim the same advantage for the method which I have had the honour of submitting to the Anatomical Society.

Dr St John Brooks also showed for Professor Cunningham, the *Centenarian Skeleton* of a Man aged 105 years. The angle of the neck of the femur was wide, and the bones of the skull, vertebral column, and sternum synostosed. The lower jaw contained some teeth, and its angle was rather oblique.

Professor Thane and the President made some remarks; and the latter said the specimen was quite unique. He possessed the femur of a woman aged 103. He observed that in this case the bones had upon them outgrowths due to ossification of tendons. As life advanced bone was laid down on the exterior with some removed from interior. The specimen also showed that rheumatoid arthritis was not incompatible with long life. The bones were decidedly heavy. Well developed and tall people lived the longest.

Messrs Anderson and Makins read their paper on *Experiments on Cranio-Cerebral Topography*, which will be found in full on page 455 of the *Journal*.

The investigations were undertaken with a view to the elaboration of a simpler and more exact series of guiding-lines to the cerebral convolutions of the motor region, and the establishment of "local points" corresponding to certain parts of the principal fissures in this locality.

A preliminary series of observations consisted in the exposure of the dura mater by the removal of one half of the skull-cap. The

dura was carefully divided by a longitudinal incision to allow an efficient examination of the convolutions; this effected, the membrane was sutured, and an outline of the subjacent sulci was traced on its surface with a thick coloured mucilage. The skull-cap was replaced, and the head so turned as to bring the mapped-out dura in contact with the bone. In this way an imprint of the tracing was transferred to the inner surface of the bones. A series of punctures in the transferred lines now allowed an accurate estimate to be formed of the relation of the sulci to the bony case. Indications obtained by this method in six cases led to the projection of certain fixed lines, which are drawn as follows:—

1. *Sagittal*, drawn from the glabella at a level corresponding to the highest point of the orbital arch (glabellar point), to the external occipital protuberance (inion). The central point in this line is called the mid-sagittal point.

2. *Frontal*, drawn from a point (pre-auricular point) corresponding to the upper margin of the external auditory meatus, and immediately anterior to the tragus, to the sagittal point.

3. *Squamosal*, drawn from the external angular process at a level with the highest limit of the orbital arch (angular point), to a point (squamosal point) fixed at the junction of the middle with the lower third of the frontal line.

Punctures made at certain proportional distances in these lines, through which pins were introduced into the brain, resulted in the establishment of a number of focal points which may be used for the determination of the position of the most constant and important sulci in the motor region. These points were elaborated from observations made on both sides of the head in twenty cases, thus amounting to forty in number. In spite of the infinite variety of contour met with, it has been found possible so to arrange the points as to make them focal for all the probable variations, a trephine of 1 inch diameter being employed.

1. *Fissure of Rolando.*—An oblique line is taken commencing $\frac{3}{8}$ of an inch posterior to the sagittal point, carried obliquely downwards and forwards across the frontal line to a point $\frac{3}{8}$ of an inch anterior it in the squamosal line. The line so marked out was, for convenience sake, carried into the superior longitudinal and the Sylvian fissures respectively, the narrowness of the bridge above, and the varying width of the gyrus connecting the ascending parietal and frontal convolutions below, making the introduction of fixed points above and below a source of complication apparently both unnecessary and undesirable.

2. *Fissure of Sylvius.*—This follows closely the direction of the squamosal line. The varying points in its course are determined by subdivision of the line into proportional lengths. The commencement lies at $\frac{5}{12}$ of the distance between the angular and squamosal points measured from before, the bifurcation at $\frac{7}{12}$ of the same distance, while the termination corresponds to a point fixed by continuation of the squamosal line to a distance behind the frontal line equal to that

between the frontal line and the bifurcation, and continued upwards for $\frac{1}{2}$ an inch at its termination in a direction parallel to the frontal line. The division of the squamosal line into twelfths is readily effected by using a tape measure on which the inches are graduated in twelfths.

3. *External Parieto-occipital Sulcus.*—The position of this is determined by a point fixed at $\frac{7}{12}$ of the distance between the mid-sagittal and occipital points, measuring from the former. (Details as to the fixation of these points will be found in the paper on p. 455 of the *Journal of Anatomy and Physiology.*)

For the frontal and intraparietal sulci no indications of sufficient regularity for formulation could be procured.

During the course of the investigation, the desirability of obtaining some information as to the fixity of position of the various sutures and eminences in skulls of equal dimensions, at present in use as land-marks, became apparent. With a view to collecting some details on this subject, thirty normal skulls were measured, giving the following results, correction being made for the varying dimensions of the skulls (for tabulated details see p. 465 of the *Journal of Anatomy and Physiology*):—

1. Bregma from glabella. Average distance, $\frac{1}{3}$ of the length of the sagittal line; range of variability, $\frac{1}{2}$ an inch.

2. Apex of lambdoid suture from external occipital protuberance. Average distance, $\frac{1}{5}$ of the length of the sagittal line; range of variability, $\frac{7}{8}$ of an inch.

3. Highest level of squamous suture, taken in frontal line from pre-auricular point. Average distance, a little under $\frac{1}{3}$ of whole length of frontal line; range of variability, $\frac{3}{4}$ of an inch.

4. Temporal ridges in same line. Range of variability, 1 inch; average distance between upper and lower, about $\frac{1}{2}$ an inch.

5. Parietal eminence, occupies about mid-point of an oblique line, crossing its summit, carried from the pre-auricular point to the sagittal line. Range of variability in horizontal line, 1 inch; in vertical level, $\frac{1}{2}$ an inch.

6. Frontal eminence. Average distance from sagittal line, $\frac{1}{2}$ an inch; from upper margin of orbit, $\frac{5}{8}$ of an inch.

Both these eminences are often difficult to localise, even on the skull.

7. Mastoid process. Averages, $\frac{3}{4}$ of an inch in width, but varies considerably; the posterior margin also often, being obscured by the insertion of the sterno-mastoid muscle.

Most, if not all, of the convolutions and sulci, although sufficiently constant in character and position to permit of easy recognition, are often very capricious in their course. The fissure of Rolando, for example, with its limiting convolutions, may extend, even from end to end, without material deviation in the line from its upper and lower extremities, or it may, especially in the upper $\frac{1}{3}$, describe curves of such strength, that an inch trephine applied over the same line might

fail to expose the sulcus. The angle formed by it with the sagittal line, in eight cases (sixteen fissures), varied between 55° and 65°, except in one case, in which the right fissure measured 70° (the left 65°).

The same observation as to variability, of course, obtains equally well to the point of termination posteriorly of the fissure of Sylvius.

Mr Victor Horsley criticised the paper, and wished to know whether observations were made from hardened brains or fresh. He and Dr Beevor had shown that the fissure of Rolando had a well-marked genu, which marked an alteration in function, namely, arm above the knee and face below. The general variations were from the lower to the higher type. Messrs Anderson and Makins' observations required to be checked by Professor Cunningham's method. Diagrams were wrong as regards the precentral sulcus, even in the latest works on surgery.

Dr St John Brooks said the true key to any point in the brain was to take certain fixed points. Professor Cunningham's results coincided with Mr Hare's.

Mr C. B. Lockwood showed a cast and photographs, *vide* fig. 1, to

Fig. 1.

show an *Abnormality of the fissure of Rolando* which he had found in the brain of a subject, which had been brought in the ordinary way

for dissection. The history was unknown, but the brain, although small, was well formed, with simple but well-marked convolutions and sulci. The left hemisphere had no peculiarity, but the right fissure of Rolando was as follows (fig. 1):—It began above by opening into the great longitudinal fissure, and after descending downwards and forwards above an inch, bifurcated to inclose a long narrow convolution. The two limbs which embraced this convolution ended by opening separately into the posterior limb of the fissure of Sylvius. Mr Lockwood said he had never seen a similar abnormality; he was inclined to think that this "anomalous convolution" belonged to the parietal lobe. He had no explanation to offer to explain its occurrence.

Mr C. S. Sherrington read a paper upon the *Topography of the Pyramidal Tract*, in which he said that after section he had noticed that, in addition to ordinary degeneration in the pyramidal tract in monkeys, there was also a small peripheral degeneration near the surface of the cord, which had been found in ten cases. This tract seemed to have no special function, and seemed never to have been noticed.

Mr J. Griffiths read a paper on the *Anatomy of the Prostate Gland*, which is printed *in extenso* on p. 374 of the *Journal*. It went to show that the history of the middle lobe was in a very unsatisfactory state. Doubt was cast upon its existence. He himself had in a number of observations seen orifices in addition to the ordinary prostatic ducts further up the urethra. When these were present there was additional gland tissue in the position assigned to the third lobe. The middle lobe was sometimes pronounced, and had a partial capsule, derived from the capsule of the rest of the gland. The presence of the middle lobe was somewhat variable. The muscular fibres of the prostate was difficult to trace in adults, but easy in nine months' fœtus and earlier. The fibres were mainly circular and longitudinal, and continuous with those of the bladder.

Dr St John Brooks thought the ducts were an argument in favour of the separateness of the middle lobe. He wished to know how they developed.

Mr Mayo Collier read a paper, in which he endeavoured to disprove the existence of the three *Glosso-epiglottidian Ligaments*. Instead there is a distinct fibro-elastic membrane attached to the whole width of the hyoid bone in front, and to the epiglottis behind. Laterally its free margin runs outwards from the side of the epiglottis to line the fossa for the tonsil. The name hyo-epiglottic membrane was proposed for the middle part of this membrane, and the name amy-epiglottic fold for the tonsillar part. The central glosso-epiglottic ligament and the hyo-epiglottic ligament were not distinct structures, but constituted a single hyo-glosso-epiglottic ligament. The author had never been able to make out a continuous elastic membrane

between the thyroid cartilage and the hyoid bone. This paper was discussed by Messrs Sutton, Thane, and William Hill, who referred to the works of Landois, Hyrtl, Henle, His, and others upon the same subject.

It was announced that, owing to the number of papers sent in, an extra meeting would be held on March 6, at Guy's Hospital.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

MARCH 1889.

An Extra Meeting of the Society was held on March 6, at Guy's Hospital, at 5 P.M. The President, G. M. Humphry, M.D., F.R.S., in the chair. Thirty-one members and visitors were present.

Alexander Macalister, F.R.S., drew attention to the desirability of a *scheme of collective investigation*, and suggested that a committee be formed to consider the question.

J. N. C. Davies-Colley proposed, and G. D. Thane seconded the proposition, that the committee of management, with the addition of Alexander Macalister, be requested to report to the next meeting upon the subject. Carried *nem. con.*

Professor Macalister next drew attention to what he considered would be a desirable amendment of the Anatomy Act, namely, that provision should be made by which unclaimed bodies should belong to the Secretary of State. This was discussed by Messrs Thane, Humphry, Davies-Colley, John Cook, and Arthur Thomson.

Professor G. B. Howes then read his paper, *Additional Notes upon the Intra-narial Epiglottis.* This paper will be found at page 587 of the *Journal of Anatomy and Physiology.*

Dr R. L. Bowles afterwards read his paper upon *The Anatomy and Development of the Palate and Epiglottis in Animals.* This paper is printed *in extenso* at page 606 of the body of the *Journal of Anatomy and Physiology.*

After quoting Youatt, who says that "in the horse the velum forms a perfect division between the mouth and the pharynx, so that, although it yields and permits the food to pass under it, in order to enter the pharynx, it prevents the return of the food, and the horse, except in the convulsive spasms of death, breathes and vomits only through the nose," Dr Bowles proceeded to point out that many animals, classed together in Natural History, have differing forms and relations in the pharynx and epiglottis.

In the full-grown pig the velum is arranged precisely like that of the horse, but the epiglottis is of a different shape, entirely surround-

ing the opening into the larynx, and lying high up in the post-narial cavity; whereas in sheep and oxen the velum is ordinarily above and behind the epiglottis, so that air may pass freely either by the buccal or nasal openings. There are also large loose arytæno-epiglottidean folds facilitating the function of rumination. In specimens of the rabbit, the guinea-pig, and the squirrel he found the velum arranged as in the horse and pig. In Professor Cleland's Museum at Glasgow he had observed that the relations of the velum of a young lion were precisely like those of the pig, whilst the relations of the velum of the puma and tiger were more like those of the sheep, and the epiglottis of the hyæna was different from either.

Dr Bowles then proceeded to demonstrate the changes which take place after birth. Firstly, in man, he showed how the epiglottis in the suckling was much curled laterally, and how this formation protected the glottis by guiding the liquid food into lateral gutters; and secondly, in the pig, the specimens of which ranged from two weeks old to six months, showing that at first the epiglottis was in the mouth, then the palate grew downwards and pressed upon and indented the epiglottis, which was now partly in the buccal and partly in the narial cavity; and finally, at six months the epiglottis shot up behind the palate high into the post-narial cavity and the palato-pharyngei muscles, uniting with those of the opposite side, form a perfect sphincter at the upper opening of the œsophagus.

Dr Bowles further stated that he had been able to confirm the views which he had expressed in his paper at the meeting of the British Medical Association in Glasgow in August last, as to the part the tongue and epiglottis bore in relation to "stertor" in animals, and to the cause of death in "mislaid" sheep.

In the discussion which ensued Messrs Bland Sutton and Macalister joined, the latter showing frozen sections of the human head to demonstrate the proximity of the epiglottis to the palate.

Dr Benjamin Howard, who criticised the existing nomenclature, said he would prefer to call the free border of the soft palate, the "meridian line." Then the intra-narial epiglottis might be called the "supra-palatal epiglottis," and the ordinary position might be called "infra-palatal epiglottis." The supra-palatal cavity and infra-palatal cavity of pharynx would be a distinction which would greatly facilitate definition. This he would explain in detail in a future paper. Supposed fatal suffocation in animals from mere supine position he did not believe in. If, in frantic struggle to rise, there was extreme head flexion, this, by pressure of descending hard palate, might force body of hyoid and base of tongue backward and downward upon epiglottis, and thus suffocation might be fatal. Mere opening or shutting of mouth had nothing to do with position of tongue. Distance from genial symphysis to body of third vertebra, point of contact of dorsum, was in either case as unchanged as distance between handle and hinges of door, whether open or shut.

He called attention to references in last number of Society's *Journal*, given by Dr Bowles, to two papers he had not published.

Mr Gordon Brodie then read the following paper on *Some Observations on the Ligaments about the Shoulder*:—

1. *Transverse-humeral*, which exists in Man as a broad strong band, trapezoid in shape, passing from the greater to the lesser tuberosities of the humerus, and so roofing in the bicipital groove and causing the tendon to play in an osseo-aponeurotic canal. It is much better marked in the fœtus than in the adult, and thicker in proportion to the relative size of the bones. Microscopy reveals in the outer wall of this canal a degenerating tract of fibro-cartilage.

It is well marked in lions, bears, tigers, and apes, though in the latter it is not limited to the bone above the epiphysial line, as it is in human specimens, both fœtal and adult.

In the Musk Ox, instead of this ligament there is a process of bone joining the summits of the two tuberosities, and thus completing a foramen—the bicipital foramen. Hence we get a complete series from the osseous tunnel of the Mole to the osseo-aponeurotic canal of Man. The lower part of the Gibbon's humerus has a well-marked fibrous septum filling in the supra-condyloid foramen, and completely separating the anterior from the posterior surfaces of the bone.

2. The *coraco-acromial* ligament always presents three portions—two strong fibrous marginal bands and a thin membranous part in the centre—which rarely has many ligamentous fibres running in it, and is almost always deficient towards the coracoid process, and through this opening the pectoralis minor passes on its way to the capsule, when it misses its insertion into the coracoid process.

3. The coraco-humeral ligament, in addition to the usual description, has an *accessory band* passing from its inner edge to the margin of the glenoid cavity, its posterior aspect thus making a Y-shaped ligament with its thicker limb attached to the greater tuberosity of the humerus.

4. In the dissecting-room of the Middlesex Hospital this year there have been several instances of the tendon of the supraspinatus giving off from its anterior margin a slip which, instead of going into the capsule (as usually described), became continuous with the ascending slip from the pectoralis major, also described as passing to the capsule. In one case there was a complete separation of the muscle externally into an upper (coracoid) portion, which ended early in tendon, and a second lower (spinous) portion, which was much more muscular. One or two specimens possessed this distinct tendonous slip almost equal in size to that of the biceps tendon, and there was a partial subdivision of the muscle. A distinct bursal sac existed round the tendon in one specimen, and another had both the slip from the supraspinatus and pectoralis major anchored close together on the lesser tuberosity.

This paper was discussed by the President, G. D. Thane, and Bland Sutton.

The following were elected members of the Society:—W. E. Hoyle, Seymour Taylor, and F. G. Parsons.

MAY 1889.

A MEETING of the Society was held on May 30, 1889, at the Inns of Court Hotel, at 4.30 P.M. The President, G. M. HUMPHRY, M.D., F.R.S., in the chair. The minutes of the previous meeting were read and confirmed. The following report of the sub-committee was adopted:—1. That a committee be formed to suggest a plan by which collective anatomical investigation could be conducted, and to propose suitable subjects. 2. That the following gentlemen be asked to serve upon the committee, with power to add to their number:—Alexander Macalister, F.R.S.; John Cleland, M.D., F.R.S.; Arthur Thomson, G. B. Howes, and Peter Redfern. The following were elected members of the Society:—W. H. Haslam, H. C. de Renzi, Arthur Robinson, John W. Smith, Clement Lucas, Stanley Melsome.

Nares and Epiglottis.

Dr SYMINGTON showed a series of specimens and drawings of mesial sections of human fœtuses from the fourth to the ninth month; also similar sections in infants. The majority of the sections were made on the frozen subject, but some of the smaller fœtuses were cut with a knife after being hardened in spirit and embedded in paraffin. In a nine months' fœtus, which was frozen with the head flexed, the epiglottis projected upwards behind the soft palate. In all the other specimens there was a distinct interval between the tip of the uvula and the upper end of the epiglottis. Dr Symington stated that he had never seen an intranarial epiglottis in the human fœtus or child when the head was so placed that the face looked directly forwards. There was a very distinct interval between the epiglottis and soft palate in fœtuses of about the fourth month. This was probably partly due to the small size of the epiglottis at that age. In the frozen section of a male gorilla, about two years old, which was exhibited, the relations between the epiglottis and the soft palate were practically the same as in the human subject.

Professor G. B. HOWES said his own observations on the intranarial position of the epiglottis were made upon the Quadrumana. His information as to the human subject was given him by Mr Bland Sutton. It was not in harmony with the statements of other observers.

Mr BLAND SUTTON said he would not be responsible for the statement that the epiglottis was always intranarial in the human fœtus, although it often was in the fifth month of intrauterine life.

Elbow-Joint.

Professor CUNNINGHAM showed three models of the fully flexed elbow-joint. They represented two longitudinal sections through the joint —one through the articulation between the humerus and radius, and

the other through the articulation between the humerus and ulna. He explained that only in the case of flexed joints were models of the sectional anatomy of the limbs useful, because in other cases the specimens themselves could be preserved so easily. The tension of the parts, however, in a fully flexed joint rendered it a matter of great difficulty to preserve, after section, all the parts in their proper position, and hence the value of models prepared when the specimens are still in the frozen state.

The models which were now submitted to the Society showed a number of interesting points. Of these, he specially drew attention to the position of the bones, and the synovial pads of fat. Although in a state of full flexion, the tip of the coronoid process was separated by a considerable interval from the bottom of the coronoid fossa; so also the head of the radius is distant about a quarter of an inch from the bottom of the radial depression. Three wedge-shaped synovial pads of fat occupy the three fossæ on the lower end of the humerus.

Professor MACALISTER considered that the ingrowing synovial processes in the humero-radial articulation were homologous to the intra-articular fibro-cartilages of the knee.

Specimen of Abnormality of the Heart and Great Vessels.

The specimen, which was shown by Mr H. C. DE RENZI, was taken from a child aged nine months. The leading features of the case are:—

1. Thickness of the muscular wall of the right ventricle as compared with that of the left;
2. The imperfect septum between the ventricles.
3. The origin of a large vessel from the right ventricle, which was continued as the descending thoracic aorta; and
4. This vessel giving off a pulmonary artery.

As to the comparative thickness of the right ventricular wall, this is doubtless to be accounted for by the greater amount of pressure which the ventricle had to overcome, and the increased amount of blood which it had to propel; at the same time, it must be remembered that although in the full-grown child and adult the wall of the left ventricle is considerably the thicker, in the fœtus, and, indeed, up to seven or eight days after birth, when obliteration of the ductus arteriosus takes place, the wall of the right ventricle is quite as thick as that of the left, a peculiarity which may be connected with the function of the right ventricle to propel the blood of the fœtus through the extended course of the ductus arteriosus, the descending aorta, and the placental circulation.

With regard to the communication between the ventricles, it will be noticed that the development of the septum has ceased at the point where it usually does in almost all cases presenting this condition, namely, close to the base of the ventricles.

Division of the arterial bulb, although arising by an independent process, does not take place until after some advance has been made in the division of the originally single ventricle; it is possible, there-

fore, that the inter-ventricular septum had not yet reached the stage when it would be necessary for the efficient working of the heart that division of the arterial bulb should take place, and thus produce a separate vessel for each ventricle.

The septum of the arterial bulb was not developed at all, and there was a persistence of the entire left 5th branchial arch.

A Rare Form of the Transversus Nuchæ.

Mr J. F. Clarke then described the above. The first regular description of this muscle is that of Schulze (Schmidt's *Jahrbuch*, B. 127, p. 288).

Schulze estimates the frequency of its occurrence at 18 out of 25 subjects. Macalister, in his "Catalogue of Muscular Anomalies," printed in the *Irish Philosophical Transactions*, gives, in Irish subjects, the frequency as 7 in 20.

The muscle arises from the superior curved line near the external occipital protuberance. The various modes of insertion are given by Macalister in the paper referred to, as follows:—

"1. Into the outer part of the superior curved line.
2. Into the posterior border of the sterno-mastoid.
3. Into the retrahens aurem, with or without an intervening tendon.
4. The muscle may be beneath the trapezius, and be inserted—
   a. With the splenius capitis.
   b. „ splenius.
   c. „ sterno-mastoid.
   d. „ retrahens aurem.
5. The fibres of the muscle interlace with those of the trapezius at its occipital attachment."

The muscle is always symmetrical. In the specimen which forms the subject of the present paper, the muscles do not correspond with any of these descriptions, though this arrangement may have been noticed since the works referred to appeared.

On both sides the muscle is inserted by a broad fan-shaped group of fasciculi into the angle of the mouth. Both muscles are of a double digastric form.

On the right side the muscle arises by two heads from the ligamentum nuchæ 4 inches below the external occipital protuberance. The two heads pass to a common tendon placed over the sterno-mastoid. From this tendon two other bellies spring anteriorly, and spreading out unite, and at the angle of the mouth join the bundles of the risorius and platysma.

On the left side one of the two posterior bellies arises from the outer end of the superior curved line, the other from the ligamentum nuchæ; in other respects it resembled the muscle on the right side.

The muscle was supplied by the 7th nerve.

The muscles differ so widely from the transverse nuchæ, as it is commonly seen, that at first I thought it might be an abnormal

risorius; the latter, however, is seen well developed, and arising superficial to the anterior part of the muscle described above.

I am indebted to Dr Macalister for the references given in this paper.

Professor CHARLES STEWART next showed a dissected specimen of a *Cutaneous Fold from the Neck of a Goat.* The interior of the fold contained a rod of yellow elastic cartilage. He looked upon the fold as being a supernumerary auricle.

Mr BLAND SUTTON had also seen a cartilaginous rod in these supernumerary auricles, and also fibres of the platysma.

Mr SHATTOCK had found a piece of similar cartilage in a supernumerary auricle from a child's neck.

Mr ARTHUR THOMSON next read his paper on the *Influence of Posture on the Form of the Tibia in different Races of Man and the Higher Apes.* This paper is printed in full at page 616 of the body of this *Journal.*

Mr SHATTOCK said that he and Mr Parker had described the astragaloid facet in connection with club-foot, and attributed it to flexion of the muscle.

Lumbar Curve in Spine of Gorilla.

Dr SYMINGTON showed the spine of a young gorilla to demonstrate the existence of a lumbar curve. The animal had been frozen with the thighs extended, and then cut in median sagittal section. There is both a lumbar and a dorsal curve.

Professor D'ARCY THOMPSON showed a number of specimens of *Fishes' Skeletons* to illustrate a cheap method of mounting them on glass.

It was announced that the next meeting would be held at Leeds, on Thursday, August 15, at 4 P.M., in the Anatomical Theatre.

After the meeting, the members of the Society entertained the President, G. M. Humphry, M.D., F.R.S., at dinner. The Chair was taken by Sir William Turner, M.B., F.R.S., and seventy-two members and visitors were present; amongst the latter were Sir James Paget, Bart., F.R.S.; Sir Joseph Lister, Bart., F.R.S.; W. S. Savory, F.R.S., President of the Royal College of Surgeons; John Marshall, F.R.S., President of the Medical Council; Professor Michael Foster, *Sec.*R.S.; R. K. Parker, F.R.S.; and W. H. Flower, C.B., F.R.S.

INDEX TO PROCEEDINGS OF ANATOMICAL SOCIETY.

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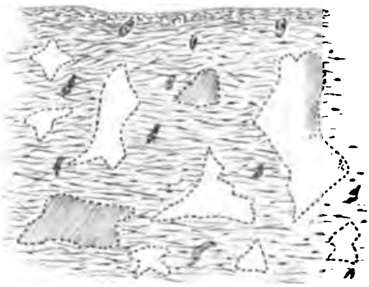
A

B

C

D



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